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TERRITORIALITY AND SOCIAL BEHAVIOUR IN A TEMPERATE ZONE PACIFIC GOBY, *CORYPHOPTERUS NICHOLSI*

by

© KATHLEEN SABINA COLE

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY
DEPARTMENT OF
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Date 21 May 82

This thesis is dedicated to
Sabina and Randal for their love and support,
and
to the people of Bamfield
for their friendship and generosity

Abstract

C. nicholsi is a temperate zone marine goby. It occupies subtidal rock-rubble habitat in protected waters, along much of the Pacific coast of North America. All members of the population occupy the same habitat, and defend space throughout the year. Peripheral overlap of territories was common, particularly between fish of different sizes. However, each territory had a central area containing a refuge that was not overlapped by territories of other fish. For small fish, this central area was usually located in the interstices of territories of large fish.

Access to space was regulated by direct aggression and effects of dominance. Fish defended their territories against codominants and subordinates. As dominance and size were directly correlated, large fish controlled the use of most of the available space.

Reproduction by *C. nicholsi* is typical of many gobiids. Gravid females entered the territory of a courting male, oviposited on the roof of the nest chamber, then returned to their territories. The males guarded the eggs until hatching. Females consistently spawned with the most dominant courting male. Females apparently based their choice of spawning partner on the vigour of courtship. Dominant males tended to court most vigorously, and may have suppressed courting behaviour in subordinate males. Males in the laboratory sometimes guarded more than one set of eggs at a time. In natural populations, males are probably polygynous.

Small males did not court females, but may have engaged in sneak spawning. Testes of small males were proportionately larger than those of large males, and small males were often found in close proximity to spawning pairs.

C. nicholsi also demonstrates protogynous hermaphroditism. Sex change in females may take several months, and in laboratory populations, occurred both in the presence and absence of large dominant males. In intersexual gonads, spermatic tissue first developed around the ovarian lumen, then replaced degenerating ovarian tissue. All testes examined appeared identical in structure, suggesting that all males are secondarily derived from females, in this species.

Territories of *C. nicholsi* were shown to be multifunctional. Territories provided a site for feeding, for reproduction, and for refuge. However, neither reproduction nor defence of a food resource appears to be solely responsible for territorial behaviour. In laboratory and field populations, territories were centered around cover, and in laboratory experiments, cover was important in determining territory location. Refuge, in the form of excavations under rock, is probably the major resource requiring territorial defence in this species.

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General Introduction

Social organization of site-attached fishes has received much attention in the last two decades. Studies have examined social structure at the community level (Sale 1974, 1975; Itzkowitz 1978) as well as at the individual level (Keenleyside 1972, Reese 1973, Ross 1978, Larson 1980, Nursall 1981), and conclusions have been expressed in both ecological and behavioural terms. It is clear that many factors affect social organization, including resource abundance and defensibility of limiting resources (Thresher 1977), modes of reproduction, forms of social relationships among interacting conspecifics (Scott 1956), and caste structure within populations (McBride 1964).

The majority of territorial fishes studied has been inhabitants of coral reefs, where conditions are conducive to long-term observations of natural populations. In comparison, relatively few extensive studies have been done on site-attached fishes of the marine temperate zone, although this is changing (Clarke 1970, Stephens et al 1970, Brown and Green 1976, DeMartini 1976, Moran and Sale 1977, Larson 1980).

The shallow (0-15 m depth) subtidal zone of the Pacific northwest has a rich and diverse fish fauna about which remarkably little is known. This area offers many opportunities for the examination of social systems of temperate zone site-attached fish.

Coryphopterus nicholsi (Bean), the blackeye goby, is a temperate zone marine goby. Individuals inhabit protected subtidal rock-rubble habitat from Baja California to the Queen Charlotte Islands (Bohlke and Robins 1960, Hart 1973). In the northern part of its range, it is one of the most common inhabitants of rocky inshore waters and is described as being territorial (Hart 1973, Wiley 1973). However, few studies have been carried out on this species.

The purpose of this study was to examine several aspects of social organization in the blackeye goby. First, I wished to describe the spatial distribution of *C. nicholsi* with regard to territoriality. Second, I wished to examine social behaviour associated with space defence and determine social mechanisms whereby space is acquired and maintained. Third, I wished to determine how social organization and space defence are influenced by reproductive processes. Finally, I wished to determine what resource(s) may be important in determining a territorial social organization in this species. The results of this study have been organized into five papers. The first paper examines features of territoriality in a field population. The second paper investigates patterns of spatial partitioning in laboratory populations. The third paper describes the occurrence of protogynous hermaphroditism in *C. nicholsi* and discusses consequent implications on interpretations of the adaptiveness of the social structure of this species. The fourth paper examines reproduction in *C. nicholsi*, and in particular, the influence of individual features of males and their territories on male reproductive success. The last paper examines the question of resource defence. In it, preceding findings are reviewed, and new information is presented which offers suggestions for the adaptive significance of territoriality in *C. nicholsi*.

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I. Paper 1. Patterns of Space Use in a Field Population of *Coryphopterus nicholsi*, a Marine Goby

A. Abstract

Coryphopterus nicholsi is a temperate zone marine goby that occupies rock rubble in protected subtidal areas along the Pacific coast of North America. In field populations, fish of all sizes and both sexes are found in the same habitat. All defended space during both the reproductive and the non-reproductive season. Aggression was invariably directed at same-size or smaller fish, suggesting the presence of a size-related dominance hierarchy. Territories showed peripheral overlap, usually with conspecifics of different size classes. Territory size was directly correlated with fish size, but was unaffected by season. Social organization in *C. nicholsi* appears to be defined by territorial behaviour and dominance relationships among adjacent individuals.

B. Introduction

Patterns of spatial partitioning among solitary, territorial fishes have received much attention in recent years. However, the majority of studies has been on tropical and subtropical marine fishes that are primarily associated with coral reefs (Keenleyside 1972, Myrberg and Thresher 1974, Sale 1974, Thresher 1976, Reese 1978, Robertson 1979, Nursall 1981). In warm-water marine fishes, territorial defence is often restricted to one sex (usually parental males) or to one age class (often adults) and the pattern described most frequently is one of exclusive territories. Such territories are defended for purposes of reproduction, feeding, or both.

Territories used solely for reproduction are usually defended by older males in a population, either on a part-time daily basis, as with some broadcast spawners (Robertson and Choat 1974, Barlow 1975a) or for the period of time required for eggs to hatch, as with some planktivorous damselfish (Swerdloff 1970, Myrberg et al. 1967, Fishelson et al. 1974). Juveniles and floaters reside elsewhere, in groups or in suboptimal portions of the habitat, and opportunistically move in when a vacancy occurs.

Feeding territories of reef fishes are usually defended on a more permanent basis (Low 1971, Sale 1974). Juveniles may settle in the optimum habitat, exist interstitially between territories of adults (Nursall 1977), and subsequently expand their spaces as their size and their needs increase, and as territory boundaries shift around them due to loss and immigration.

Considerably less information is available on the territoriality of temperate zone marine fish. In some cases, territorial behaviour has been found to be seasonal (Carlisle 1961, Hixon 1981), and not always associated with reproduction (Brown and Green 1976). However, information on a few species of permanently territorial fish suggests that some temperate zone marine fishes may demonstrate considerable diversity and complexity of social organization related to site defence (Clarke 1970, Moran and Sale 1977).

Coryphopterus nicholsi, the blackeye goby, is a temperate zone marine fish having a range extending from Baja California to the Queen Charlotte Islands of British Columbia (Hart 1973). Individuals occupy the shallow subtidal region along protected rocky shores, and are reputed to demonstrate year-round territoriality (Wiley 1973), but no detailed information is available. The present study was undertaken to examine spatial and behavioural aspects of territoriality in a field population of *C. nicholsi*. Four questions were addressed: 1) what members of the population defend space? 2) how is space partitioned among individuals? 3) is space defence of *C. nicholsi* seasonal or year-round? and 4) if territories are long-term, are border locations and territory size unchanged among individuals during the reproductive and the non-reproductive season?

C. Methods and Materials

Study area

The study area consisted of a subtidal rock rubble patch measuring approximately 8 x 60 m, situated at the entrance of Bamfield Inlet, off Barkley Sound (latitude 49 N., longitude 125 W.) on the west coast of Vancouver Island, British Columbia. Station records indicated that the site chosen had not been disturbed by previous studies, and its accessibility during winter storms allowed for regular winter observations.

The rubble patch consisted of various-sized rock (5-45 cm diameter) on a bed of sand and finely fragmented shell. The rubble patch was bounded above by a *Nereocystis luetkeana* bed (0-4 m depth) and below by a sloping silt plain (12 m + depth).

Four quadrats measuring 2 x 2 m and divided into four equal sectors were set one meter apart, along a depth contour 7 m below mean low tide. Fish were observed within these quadrats.

Method of observation

Underwater observations on individual fish were carried out between December 1979 and July 1980, using SCUBA . With another observer, a total of 54 hours of observation were made. A series of four 40-minute dives on four consecutive days was made approximately every two weeks over an eight month period. During these four dives, each observer carried out observations on two quadrats, restricting recording to one quadrat per dive, resulting in a total of 80 minutes of observation for each quadrat over the four-day series. Dives were carried out at slack low or slack high tide, whichever occurred during the morning daylight hours.

Data were collected by observing all fish within a single quadrat for 40 minutes. Activity was generally low enough to permit this method of sampling. A substrate map showing the location of rocks and sand-shell patches was used on which to record the movements of fish and location of various activities. In this manner, the frequency and the range of specific activities were recorded, and from the latter, areas of activity were determined.

One night dive was carried out over the study site; strong night lights were used to locate gobies and record their activities and positions.

An additional 40 hours of general observations were carried out between April 1977 and November 1979. Notes were made on presence or absence of gobies in various habitats, including kelp beds, steep rock walls along inlets, on protected sides of small islands, and habitats with substrates of silt, sand, or large boulders. In addition, unbaited minnow traps were set out at various depths from 3 to 13 m in these habitats, and checked periodically.

Identification of individuals

Identification of individuals by tagging with subcutaneous dye injections was initially tried on fish from another site, but over 80% of the tagged fish (n=17) disappeared within two days and were not seen again during the next four months of observations. As I wanted to carry out observations on a relatively undisturbed population, other means of identification had to be used. Individuals possessing natural markings, such as split or notched fins, body scars, or unusual pigment marks, were individually identified more readily than those without such marks. In the latter case, behavioural idiosyncrasies such as the defence of consistent borders from dive to dive, habitual perching on a certain promontory within an area of activity, or following the same route between two covers or a cover and a promontory (an activity of high frequency), were all used to aid in identification. However, not all individuals were clearly identifiable from observation to observation. For this reason, fish were assigned to one of three size classes: small (approximately 25-55 mm standard length), medium (approximately 55-70 mm SL) and large (70 mm + SL), and subsequent data were handled on the basis of size groups rather than individual fish.

Behaviours recorded

The initial selection of behaviours used to record activities of fish were based on behaviours observed in laboratory fish (see Paper 2). The location and the frequency of the following territorial, reproductive and maintenance behaviours were recorded during field observations.

"Approach" occurred when one fish rapidly swam towards a conspecific. "Avoidance" consisted of one fish moving away from another. When an approaching fish elicited avoidance behaviour on the part of a conspecific, the first fish was said to have displaced the second.

"Attack" involved biting or attempted biting by one fish after rapidly approaching another . This usually occurred only when an approached fish did not demonstrate avoidance.

"Display" involved one or two fish, in which approach was not followed by avoid. Fins were held in an extended position, and the body colour paled from a light orange or brown tan to a cream colour. Thus, dark marks on the fins stood out in contrast. Body movements were characterized by exaggerated lateral undulations, often accompanied by mouth gaping.

"Chase" occurred when an approaching fish pursued an avoiding fish. "Sit" described a fish resting motionless on the substrate. "Perch" occurred when a fish rested on top of a rock. "Under cover" described a fish with more than half of the body (usually the caudal portion) under cover.

"Feeding" described snapping movements directed towards particles in the water column or on the substrate, followed by mouth movements, including the rejection of an item. "Hover" was often associated with feeding, and consisted of an individual briefly remaining motionless in the water column.

"Court" consisted of any of a series of movements involving displaying, approaching and leading to cover used prior to egg deposition (see Paper 4).

Data analysis

After each dive, data were transcribed from activity maps. From the location points of various activities, activity boundaries were determined. The entire area used by a fish was measured with the use of a planimeter, as well as the amount of area overlapped by territorial adjacent fish, and the exclusive (i.e., unshared by conspecifics) portion of each individual area. Rates of aggression were also calculated.

The data were then organized according to quadrat, the time of year, and size of fish. The eight months of data were divided into four approximately equal time periods; December, January-February, April-May, and June-July. The last two time periods covered most of the reproductive season, which lasts from March to July (see Paper 3). Each time division represented approximately 200 minutes of observation per quadrat. Comparisons of the the size of the area of activity were then made, using size of fish and the time of year as factors (three-way factorial analysis).

Small fish were more difficult to see, and more secretive in their behaviour compared to medium-sized and large fish. Activity rates were correspondingly low, and areas of activity for individuals in this size group were not calculated.

Population structure

Gross sexual dimorphism in *C. nicholsi* is restricted to differences in the structure of the genital papilla (Wiley 1973). Therefore, the sex of a given fish could not be determined unless courting or spawning was observed. Fish from the four observation quadrats were collected with the use of the anaesthetic 2-phenoxy-ethanol and a slurp gun, at the end of the observation period (July 1980), so to obtain accurate information on the sex and size of individuals observed over the previous eight months.

D. Results

Fish distribution

Coryphopterus nicholsi was found in the greatest abundance in patches of rock rubble interspersed with sand-shell in shallow, protected waters, usually between 3 and 15 m below mean low tide. Rock rubble habitat along the coast is discontinuous. In its absence there may be sand or silt plain, large boulder and rock-slab field, or kelp bed. The transition from rock rubble to another habitat is usually abrupt.

C. nicholsi was never sighted on boulder and rock slab substrate, and trapping in these areas was always unproductive. Occasionally, very small fish were seen on rock-free areas adjacent to the rock rubble patches, but when startled, they fled in the direction of the rock patch. Fish were occasionally sighted and trapped in kelp beds, but the frequency of these occurrences indicated that population densities in that habitat were low. *C. nicholsi* appears to prefer rock rubble and sand shell, and is largely restricted to that habitat.

Within quadrats, fish of all sizes were seen throughout the year. Seven large and four medium-sized fish bearing natural tags and followed over the eight month period maintained the same area of activity, demonstrating prolonged site fidelity. During the reproductive season, spawning and egg-guarding were frequent events within these same sites.

Few fish were seen at the periphery of the rubble patches; they were usually small and transitory. However, small and medium-sized fish were abundant in the quadrats among the adults (Table 1). Although small fish were difficult to identify, their individual use of the same cover appeared to be less consistent than that of medium and large-sized fish. The location of areas defended by these small fish also varied more than that noted among the medium and large-sized fish. The number of large transient fish recorded on the study site was small. Generally such transients remained in a quadrat for only one or two days. Only one case was recorded in which a territory was clearly established and defended; abandonment occurred, however, within the first month.

Behaviour

Duration of behavioural states was not recorded, so information on the amount of time spent on different activities within areas of activity is not known. However, the locations where various behavioural events (e.g., feeding, under cover, perching and sitting) occurred indicated that such activities were most frequently conducted close to cover (an example is seen in Fig.1). Activities associated with cover consisted of perching on a promontory or sitting on the substrate; preferred locations of sitting or perching were consistent over time.

Feeding movements consisted of rapid forays from a resting spot, followed by a return to a position near shelter. Approach and attack behaviours were often directed at intruding fishes near the periphery of the area of activity. Typically, the area of activity was defined peripherally by feeding and aggressive events, as well as perching, and appeared aquivalent to a defended area.

Chase by one fish resulted in avoidance by the other. Following a chase and avoidance sequence, the aggressor would sink to the substrate for 2 to 10 seconds, then rapidly return to a frequently used perching or resting site. Lack of avoidance generally resulted in escalation to displays, including fin erection, branchiostegal membrane extension and mouth gaping, lateral displays, and tail beating. If avoidance still did not occur, the sequence finally escalated to biting, whereupon one of the fish rapidly showed avoidance behaviour. Aggressive displays generally occurred on the border of two adjacent areas of activity of equal-sized fish. Such defence of areas of activity by fishes was considered territorial behaviour.

Aggression was invariably directed only at same-size or smaller fish. The presence of a larger fish within the defended areas of activity was generally unchallenged, and any challenges observed were usually unsuccessful. Therefore, behavioural interactions between fish of the same and different size classes strongly indicates that size regulates aggression in this species, and this in turn suggests that size may be an important factor in social dominance within field populations. Large fish had a higher frequency of initiated aggression than did medium-sized fish in each quadrat, regardless of the time period (Table 2). Although there was a significant effect of fish size ($p<0.01$) and of quadrat ($p<0.05$; three factor analysis of variance) on the frequency of initiated aggression, there was also an interaction effect between these two factors ($p<0.05$). The source of interaction may arise from the very high values of aggression found in large fish in Quadrat 4. This quadrat had more large fish on it than did the other quadrats which may explain the elevated levels of aggression.

Territory distribution

Territory (i.e., defended area of activity) maps show that territories of adjacent fish frequently overlapped (Fig.2). However, overlap was mainly on the periphery of defended areas, and cover was rarely included in the overlapped area. In 116 areas of activity where the location of 129 covers were used for shelter by defending fish were known, in only 7 instances was cover in the area of overlap; in two such cases, a second cover was located in the exclusive portion of the defender's territory.

Because of peripheral overlap, between 5 and 20 per cent of the entire territory was shared by conspecifics, for both large and medium-sized fish. Fish overlapped less with conspecifics of the same size class (i.e., large with large), than with those of a larger or smaller size class (Table 3).

Small fish occupied a shelter and defended a small area around it. Shelter was often interstitial to the activity areas of larger fish, or on the border between two areas of activity. Frequently, when a small fish was chased from the area of activity of a larger fish, the small one would simply move to an area overlapping that of another fish. In this way it avoided permanent displacement by larger fish. However, it would also defend the area within which it was found against same-size or smaller fish.

The entire territory was the total area occupied and defended by a fish. The exclusive area of a territory was that portion not used by any other conspecific.

The entire areas of territory for both large and medium-sized fish were unaffected by season ($p>0.75$) or quadrat ($p>0.25$; three-way factorial analysis of variance), but overall, large fish had consistently larger territories than did medium-sized fish ($p<0.001$). This difference was significant for each two-month observation period (Fig.3a).

The exclusive areas of territory, as with the entire territory areas, were consistantly greater for large fish than for medium-sized fish ($p<0.05$, t-test). However, the size of the exclusive area was also strongly affected by season ($p<0.001$) (see Fig.3b), and there was an interaction effect between fish size and quadrat ($p<0.05$).

Nocturnal activity

During a single night dive in June of 1980, approximately 400 m², including the four observation quadrats, were scanned for the presence of *C. nicholsi* . In an area that contains an estimated 2000 to 3000 gobies (based on daylight counts of small areas) only one goby was seen; it was partially under cover. On the four study quadrats, known retreat spaces were examined. The majority of those that light penetrated contained a single goby, located at the rear of the excavated chamber. There was no evidence of nocturnal sharing of refuge. Thus, it appears that *C. nicholsi* is strictly diurnal, and uses cover as a nocturnal retreat.

Population structure

With the use of anaesthetic, 84 fish on quadrats 1-4 were collected (Table 1). The size range and sex ratio were similar to that of population estimates from trapping collections (see Paper 3), except for a greater number of very small fish obtained by anaesthetic collection methods. The average number of fish per m² on observation quadrats was 5.3±0.6, based on the anaesthetic collection. This compared to 6.0±0.9 fish per m², based on visual counts from underwater observations.

E. Discussion

Territorial behaviour is characterized by the defence of space (Noble 1939) or by socially mediated exclusion of individuals from an area (Brown 1969) which may be fixed or floating (Wilson 1975). However, when examining natural populations under conditions that restrict observation time, defence-associated aggression can often be too infrequent to delineate territory boundaries completely. Facing a similar problem in avian studies of territoriality, Weeden (1965) proposed the term "space of activity", which is analogous to area of activity in this study. The question remains, how close are approximations of territory boundaries to boundaries of areas of activity?

Laboratory observations indicated that all activities of individual *C. nicholsi* were primarily confined within borders defined by aggressive defence (see Paper 2). On occasion a fish left its territory for a brief, rapid rush at some particle of food just outside its boundaries, but the majority of feeding occurred within territory boundaries, as did resting on the substrate, perching on a promontory, and courting during the reproductive season. Hence in laboratory populations, the area of activity and the area of territory were identical. In field populations, the area of activity is probably a good estimate of the territory. Aggression seen in the field included rushing charges against invading fish, and prolonged display contests on borders between adjacent residents that were identical to the territorial behaviour observed under laboratory conditions.

Partitioning of space among territorial individuals in a population is generally restricted to breeding adults when territories are solely reproductive, although helpers may be present (Woolfenden and Fitzpatrick 1978, Taborsky and Limberger 1981). Adults unsuccessful at obtaining space may become wanderers or floaters (Smith 1978, Brown 1969, Clarke 1970). When individuals other than breeding adults form part of a social complex of territorial individuals, territories are often multifunctional.

Coryphopterus nicholsi of both sexes and all size classes maintained territories throughout the year in the same habitat. Territories of *C. nicholsi* were not entirely exclusive; there was a combination of peripheral overlap with other individuals, similar to that found in *Abudefduf zonatus* (Keenleyside 1972) and *Hypoplectrus* spp. (Barlow 1975b), and defence of space by newly and recently settled juveniles interstitial to larger territories as described for other species (Sale 1974, Nursall 1977, Ross 1978, Larson 1980). Whether or not these interstitial areas develop into centers of future territories, as suggested by Nursall (1977), is unknown.

Newly-settled juveniles were not actively excluded from the habitat occupied by adults. Resident *C. nicholsi* merely seemed to ignore small conspecifics. Moran and Sale (1977) found that aggression towards juveniles by adults in an

Australian temperate damselfish, *Parma microlepis*, was low immediately following juvenile settlement. This may reflect a swamping effect by juveniles, coupled with the availability of suitable in-habitat refugia, as appears to be the case with *Pomacentrus wardi* (Sale 1975). When suitable alternative habitat is absent, as with *Amphiprion melanops* where the number of anemones is limited, juveniles defend mutually exclusive territories within the boundaries of territories of breeding adults (Ross 1978). The absence of juvenile *C. nicholsi* in other habitats adjacent to rock rubble suggests that such areas are unsuitable for survival, and that alternative habitat is not available.

Peripheral overlap does not preclude territoriality (see arguments by Keenleyside 1972 and Barlow 1975b). Because of the sloping and outcropping nature of the terrain, a defending fish did not always have an unimpeded view of its entire territory, which undoubtedly contributed to the occurrence of peripheral overlap. Larson (1980) explains the presence of overlap in *Sebastes* sp. as being due to a lack of patrolling behaviour on the part of defenders. *C. nicholsi* does not patrol its territory boundaries either, but rather makes forays from a central perching or resting spot. This, in addition to topographical heterogeneity, may promote peripheral overlap.

An overlapping pattern of space use resulted from the shared use of territory peripheries, with a trend towards greater overlap between size classes. Within each size class, fish had more or less mutually exclusive territories. Despite overlap, retreat spaces were generally exclusive.

In addition to non-exclusive partitioning of space, *C. nicholsi* demonstrates a dominance component to territoriality in the field. Large fish have complete dominance over all fish within their territory. Smaller fish, as a rule, are able to exclude only same-size or smaller fish. This pattern is similar to a description of "dominions" in which areas of influence are dominance-dependent (Brown 1975). In *C. nicholsi*, the zone of overlap is used at different times, since subordinate *C. nicholsi* avoid dominants. Hence, while territories overlapped spatially, temporally they did not. In addition, subordinates managed to maintain an exclusive area, despite low dominance status, as refuge space was generally outside the territory boundaries of adjacent dominants. The importance of dominance relations among territorially-organized fish has been noted in laboratory (Greenberg 1947, Newman 1956, Chapman 1962) and field populations of fish (Newman 1956, Myrberg 1972, Larson 1980).

The apparent lack of change in territory size of large and medium-sized fish, over the eight month observation period encompassing the non-reproductive and reproductive seasons, may indicate a stable year-round social organization based on space defence. This is in contrast to some temperate zone marine fishes that exhibit seasonal territoriality, usually associated with reproduction (Moore 1970, Stephens et al. 1970) or, less frequently, feeding (Brown and Green 1976). The overall lack of change in territory size in *C. nicholsi* differs from that found in *P. microlepis*, an Australian temperate pomacentrid that is territorial all year and shows an expansion of territory area during the reproductive season (Moran and Sale 1977). The lack of expansion in *C. nicholsi* under similar conditions may reflect a lack of advantage to having a larger territory size during reproduction, or a resistance to compression, for whatever purpose or cause. However, it may also be a result of my method of grouping the data according to size class rather than by tracking individuals through time. Since males and females of all different sizes (and therefore, probably different dominance) were present on the quadrats, any individual changes in area defence would have been missed.

Year-round territoriality indicates that the resources being defended are requisites throughout the year. This may be for shelter, as suggested for burrow-living *Hypsoblennius jenkinsi* (Stephens et al. 1970), or food, or both. This question is addressed in another section (see Paper 5).

To date, the different patterns of space partitioning noted among fishes of temperate zone marine habitats, appear directly comparable to those noted in the tropical fish fauna, at least in regard to the variety and complexity of territorial social systems (DeMartini 1976, Stephens et al

1970, Moran and Sale 1977).

F. Acknowledgments

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Table 1. Standard length (mm) of fish from four field quadrats, collected over a two-day period. Q_n indicates quadrat number from which fish were collected. M is male; F is female. Fish are grouped according to size (see text). Collections were made in July 1980

	Q_1		Q_2		Q_3		Q_4	
	M	F	M	F	M	F	M	F
Large	80.7	75.0	73.5		73.4		83.2	83.8
	72.3		72.0		71.9		78.5	
	72.1		71.5				75.1	
	70.6						73.0	
							72.2	
Medium	67.1	65.9	67.4	68.9	68.2	68.7	69.8	61.8
	63.4	62.7	66.9	64.6	64.2	64.5	69.1	59.5
		60.3	66.2	62.2		62.2	67.4	59.2
		57.8	62.0	59.6		62.2	66.8	58.6
			61.2	59.0		60.4	64.5	
				57.0		59.7		
						56.8		
Small	52.8	50.4		51.0		53.8		53.5
	52.0	48.6		48.6		52.9		50.7
	49.3	47.3		47.8		47.5		48.7
		47.1		46.6		46.7		45.5
		46.0		46.2		45.4		42.2
		43.8		44.6		43.8		
		43.5		42.8		41.7		
				42.7		41.0		
				41.2				

Table 2. Mean frequency of interactions initiated by all territorial fish per 45 minute observation period. Fish are grouped according to size (standard length mm). Data are grouped into two time periods, December to February (D-F), and April to July (A-J). Q_n indicates quadrat number. M is mean; N is number of observation periods; SD is standard deviation

Fish Size	Time Period		Q_1	Q_2	Q_3	Q_4
Large	D-F	M	1.9	3.7	1.6	7.1
		N	7	7	8	7
		SD	2.8	2.9	3.5	8.1
	A-J	M	2.0	3.4	1.9	5.9
		N	9	9	9	9
		SD	1.8	3.5	2.6	5.1
Medium	D-F	M	0.7	1.6	1.6	1.1
		N	7	8	8	7
		SD	0.8	1.9	1.9	1.6
	A-J	M	2.0	1.8	1.7	1.7
		N	9	9	9	9
		SD	2.2	1.8	1.7	2.2

Table 3. Proportion of entire territory area overlapped with other large and medium-sized fish for a) large and b) medium-sized fish defending territories. Mean values are given for each time period and each quadrat (Q_1 to Q_4). M is grand mean; V is variance; Dmax and p values are based on Kolmogorov-Smirnov 2-sample test

a) Proportional overlap of large fish territories:

	With large fish				With medium fish			
	Q_1	Q_2	Q_3	Q_4	Q_1	Q_2	Q_3	Q_4
Dec.	0	0	.01	.06	.08	.01	.06	.01
Feb.	0	.05	0	.06	.08	.08	.13	.13
April	.02	.09	.07	.01	.21	.12	.15	.20
June	0	.07	.13	.18	.17	.05	.20	.12
		M=0.05	V=0.003			M=0.12	V=0.003	

Dmax=0.56 p>.05 that they are different

b) Proportional overlap of medium-sized fish territories:

	With large fish				With medium fish			
	Q_1	Q_2	Q_3	Q_4	Q_1	Q_2	Q_3	Q_4
Dec.	.18	.05	.08	.68	0	0	0	0
Feb.	.07	.13	.03	.37	0	0	.09	0
April	.09	.15	.07	.41	.07	.05	.11	.06
June	.12	.09	.13	.33	.08	0	.12	.06
		M=0.19	V=0.03			M=0.04	V=0.045	

Dmax=0.56 p>.05 that they are different

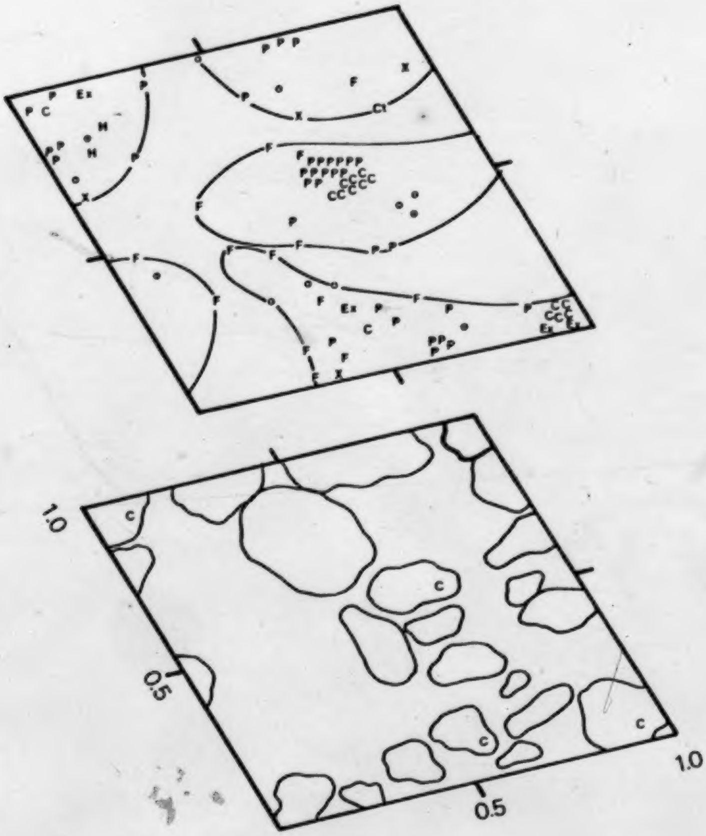
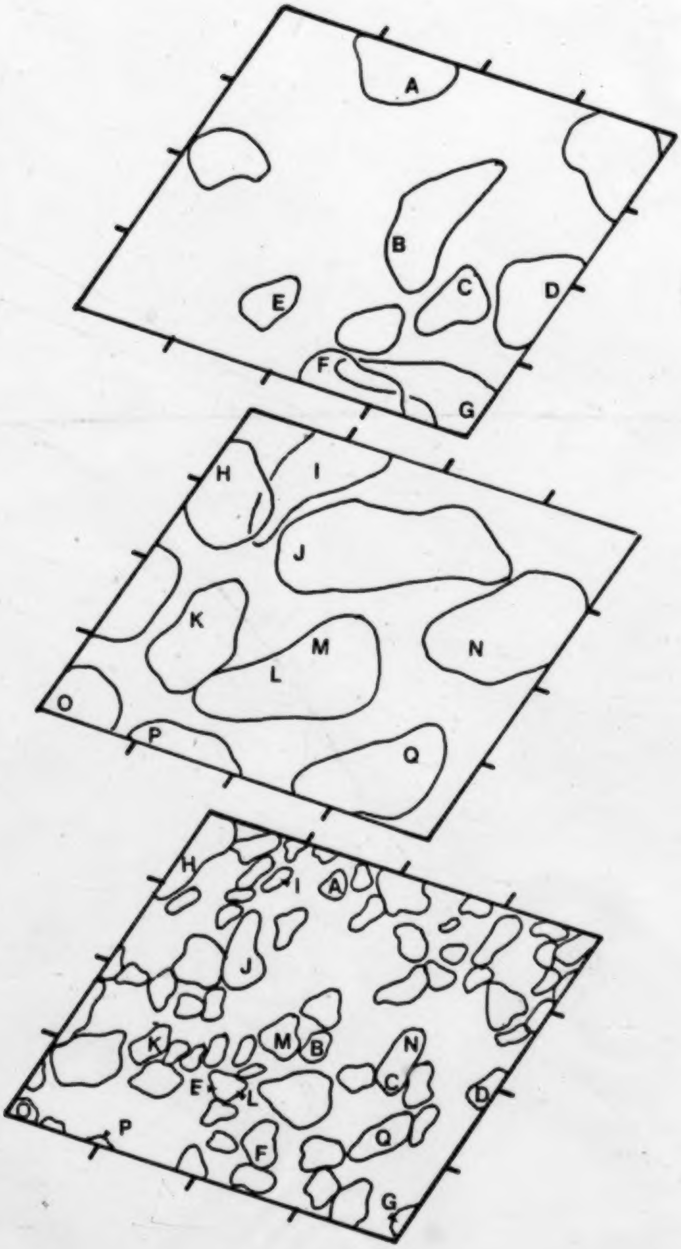


Figure 1. All activities observed in territories of large-sized fish occupying one square meter of Quadrat 4 during the April-May period, 1980. Bottom level: terrain, showing outlines of large rocks (pebbles and rocks measuring less than 5 cm in diameter are not illustrated). C indicates the location of retreat spaces on corresponding territories outlined on the upper level. Axes show grid units (m). Upper level: location and frequency of occurrence of activities of individual fish, denoted by lines. Symbols for activities are: F, feeding; P, perching on an elevated surface: o, sitting on substrate; C, under cover used for retreat; Ex, excavating sand from under cover; X, aggressive behaviour used to displace intruders; Ct, courting; H, feeding while hovering in the water column.

Figure 2. Territory maps of _C. nicholsi_ in Quadrat 4, compiled during April-May 1980. Bottom level: terrain, showing outline of rocks. Axes show grid units (0.5 m). Letters indicate rocks under which retreat spaces were excavated by territorial holders, and directly correspond with the location of letters in the territories shown on the middle and upper levels. Middle level: territories of large fish. Letters indicate the location of excavations used for retreat in different territories. Upper level: territories of medium-sized fish.


A
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C
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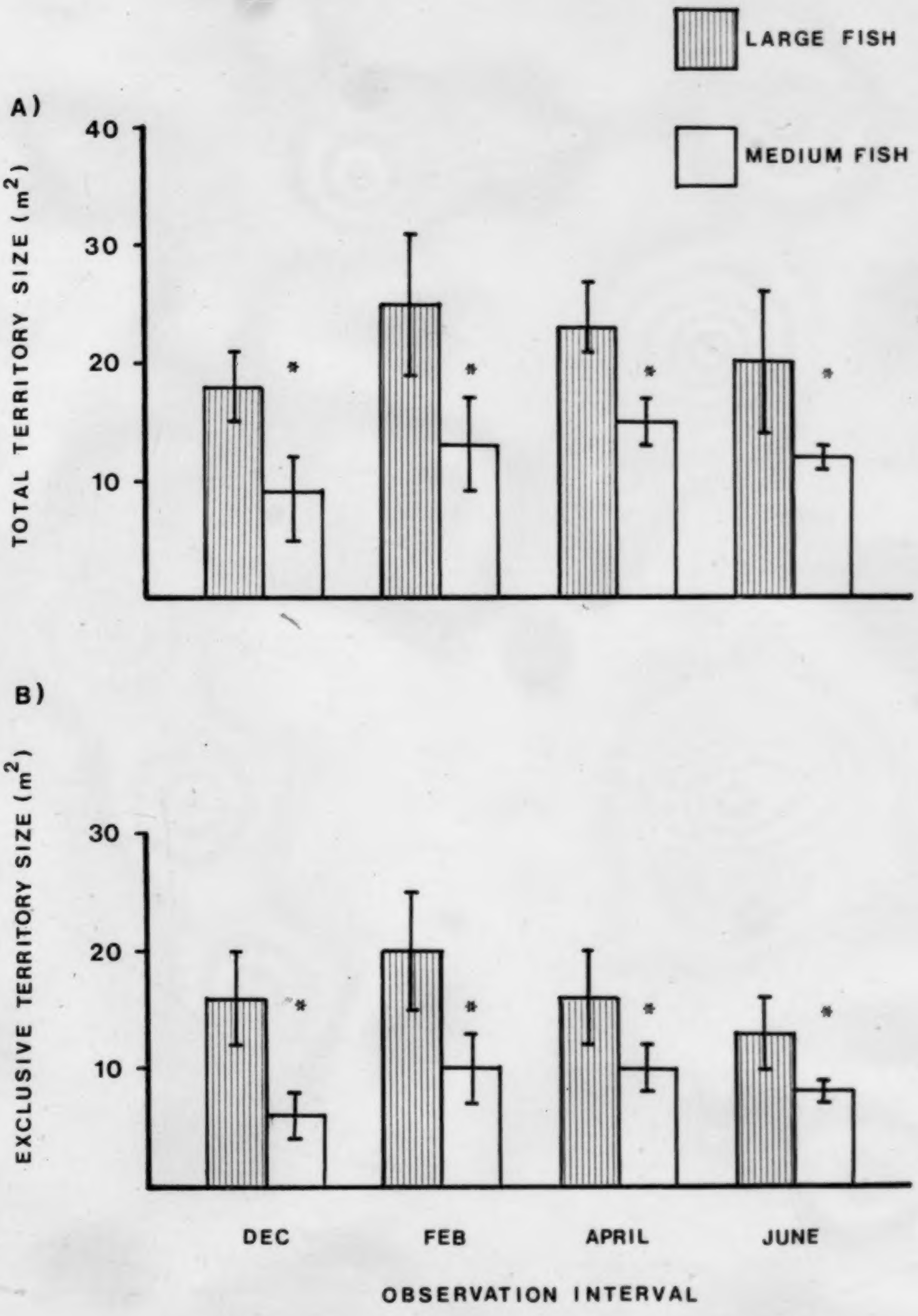
APRIL - MAY

Figure 3. Effect of season and fish size on mean territory size of individual fish for a) entire territory and b) exclusive portion of territory. * indicates significant differences between pairs of bars representing large and medium-sized fish ($p<0.05$, t-test).


LARGE FISH
MEDIUM FISH
A)
TOTAL TERRITORY SIZE (m^2)
40
30
20
10
*
*
*
*
B)
EXCLUSIVE TERRITORY SIZE (m^2)
30
20
10
*
*
*
*
DEC
FEB
APRIL
JUNE
OBSERVATION INTERVAL

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II. Paper 2. Patterns of Space Use and Social Organization in Laboratory Populations of *Coryphopterus nicholsi* (Pisces: Gobiidae)

A. Abstract

Coryphopterus nicholsi is a temperate zone marine goby. In laboratory groups of fish, territorial behaviour and site fidelity were demonstrated over a period of time lasting 10 months. Territories were not exclusive; overlap of territories occurred, particularly between fish of differing size and dominance rank. Access to space was dominance-related; dominant fish controlled the majority of the substrate and subordinate fish defended area conditionally upon the absence of a dominant. Size of fish and dominance rank were strongly correlated. Under some circumstances, size of territory and dominance rank were also directly correlated. An increase in the area of territory of dominant males was associated with the onset of the reproductive season. The presence of eggs in a male's territory resulted in increased size of the exclusive portion of the territory.

B. Introduction

Observations on natural populations of territorial fish can provide much information on the nature of space partitioning and the behaviour associated with space defence. However, in some cases conditions are not conducive to long-term underwater observations, and the tracking of untagged individual fish can be difficult. As a consequence, the social dynamics involved in the acquisition and maintenance of space, and the individual responses to seasonal and reproductive changes are difficult to discern.

Coryphopterus nicholsi is a temperate zone marine goby whose range extends from Baja California to the Queen Charlotte Islands of British Columbia (Hart 1973). Field observations in the vicinity of Bamfield Marine Station, British Columbia (lat.49 N., Long.125 W.), have shown that all members of the population, including both sexes and immatures, defend space throughout the year, apparently on a dominance-ordered basis (see Paper 1). However, individuals in the field could not be tagged without high loss rates. Therefore, tracking of individuals throughout the year was difficult. Moreover, low visibility and cold water temperatures made intensive field observations unfeasible. Under these circumstances, the relationship between characteristics of individual fish and accompanying territorial behaviour could not be easily determined.

A series of laboratory populations of *Coryphopterus nicholsi* were established to answer the following questions:

1) is site fidelity demonstrated over long periods of time?

2) how is space partitioned among territorial fish?

3) what characteristics of individual fish are associated with acquisition of space?

4) are there changes in the size of area defended associated with a change in reproductive state or dominance rank of the territory holder?

C. Methods and Materials

All experiments were carried out at Bamfield Marine Station, British Columbia. Three groups of nine fish each were established in similar pool conditions and observed for five months (Experiment 1). Three other groups of 14 fish were established in pools twice the size of that of the first three groups (Experiment 2); two of these were observed for 10 months, the other for five months. Fish for both experiments were collected in unbaited minnow traps distributed along rocky shore areas in Bamfield Inlet and off nearby islands. The sex of individuals was determined by an examination of the genital papilla (examination of the gonads of over two hundred fish showed 100% correspondence with sex determination based on papilla form). Each fish was marked by a subcutaneous injection of dye (Pelikan Drafting ink), placed individually in opaque containers having rock shelter and flow-through sea water, and maintained on a diet of fresh-frozen euphausiids. All fish were held for a minimum of two weeks prior to use, and any fish not eating, or showing signs of infection in the dye-mark area were not used. When introduced into an experimental pool, all fish were placed in one bucket and added simultaneously to the new environment.

Experiment 1

Experimental pools and fish

Two 1.8 x 0.3 m circular wading pools were divided into equal halves, each with a bottom area of approximately 0.9 m^2. A substrate of sand and small shell fragments covered the bottom to a depth of 5 cm, and rocks and bricks were added to form a continuous border around each section. Bricks were propped up on rocks to provide cover. Small stones, placed in 0.2 x 0.3 m contiguous rectangles, formed a bottom grid that was used as a guide when mapping fish movements (Fig. 1).

Unfiltered fresh sea water entered each section at a rate of approximately 2 l/min and at a temperature ranging from 10 to 13.5 C over the five-month interval. Illumination was provided by pairs of fluorescent tubes 1.8 m above each pool and connected to an outdoor photocell. Photoperiod varied in accordance with natural daylength.

Three groups of nine fish (four males and five females) were established in three of the four pool sections (Groups 1, 2 and 3, Table 1). Approximately 65% of the fish were under 70 mm SL. This was similar to the proportion of fish found under 70 mm SL in minnow trap samples.

The three groups were established on 15 May 1978 and maintained until 13 October 1978. Throughout the experiment, fish were fed flaked food (Tetra Min) daily.

Observations and manipulations

In the first week after introduction into the pool sections, displacement interactions between individuals, consisting of approach, display, chase and concomitant avoidance, were recorded. Each group was watched for 90 minutes daily. In this way, the dominance rank of individuals within each group was determined.

In the second week, hour-long observations were carried out daily on each group. The locations of activities and movements of individuals were recorded on maps accurately illustrating pool substrate topography. Activities consisted of feeding, sitting under cover, sitting on the substrate, perched on an elevation (rock or brick), and interactive behaviours consisted of approach, display, bite, chase and avoid. Territory boundaries were constructed according to points of defence and areas of unchallenged movement by the territory holder, and areas of avoidance by adjacent conspecifics. These observations were continued several times weekly for the five-month duration of the experiment. Any changes in dominance rank that occurred were recorded.

Areas of territories for each observation period were calculated with the use of a planimeter. Both the entire area of the territory and the size of the exclusive portion (i.e. the portion not overlapped by territories of conspecifics) were measured. Mean values (from all observation periods) of areas of the entire and the exclusive portion of territory were then calculated for each space-defending fish and compared with respect to dominance rank. In addition, the proportion of the entire territory size that was shared was calculated for each fish, and related to dominance rank. In two of the three groups the most dominant fish (alpha) courted females, and was successful in obtaining eggs. These fish and their eggs were subsequently removed, as was the alpha fish in the third group (also a male). Subsequent changes in dominance ranks and territory sizes of the remaining fish were recorded.

Experiment 2

Experimental pools and fish

Three undivided 1.8 x 0.3 m circular wading pools were used, each with a bottom area of 2.6 m^2 and with sand and shell fragment substrate to a depth of 5 cm. Within each pool, 14 units of cover formed by one brick propped on another were spaced at regular intervals over the bottom, and a grid of small stones 0.2 m apart was made. Fresh unfiltered sea water (9 to 10 C) flowed through each pool at a rate of 4 l/min. Photoperiod was regulated by an outdoor photocell and illumination was provided by pairs of fluorescent tubes 2.3 m above each pool.

Three groups of 14 fish (seven males and seven females) were established. An effort was made to match fish for size and sex, between groups (Table 2). Unlike Exp.1, only 15% of the fish were under 70 mm SL; the average fish size per group ranged from 74 to 78 mm SL.

Two of the fish groups were established in September 1979 and maintained for 10 months (Groups A and B). The third group of fish (Group C) was established in January 1980 and maintained for five months. For the duration of the experiment, all fish were fed fresh-frozen euphausiids once a day.

Observations

As with Exp 1, initial dominance ranks were determined in the first week of observation and continually re-evaluated on the basis of interactions recorded during observation periods. Subsequently, locations of activities of individual fish were recorded and territory boundaries were determined. In addition, the amount of cover within the entire territory and within the unshared portion of territory was recorded for each territorial individual, and occurrences of aggression initiated by territory holders were recorded.

Areas of shared and unshared portions of territories were calculated in the same way as for Exp. 1. Mean values for both the entire and the exclusive area of territories were then compared within individuals, between the non-reproductive and the reproductive seasons in the two 10-month groups (A and B). The beginning of the reproductive season was determined by the presence of courting behaviour within laboratory groups of fish. Because the five-month group (C) was established so soon before the onset of the reproductive season, it was omitted from these comparisons. Similar between-season comparisons were made for the number of cover defended and the number of aggressive acts initiated per minute of observation. During the reproductive season, the undersurfaces of bricks in all three groups (A, B and C) were frequently checked for the presence of eggs, to determine spawning success. The presence or absence of eggs was then correlated with territory size.

In late January 1980, all fish from the two 10-month groups were removed from their pools, re-measured to note changes in standard length, then returned to their respective pools. In late March 1980 and in mid-July, at the end of the experiment, the procedure was repeated for all three groups.

D. Results

Experiment 1

General

Territorial behaviour was demonstrated by approximately 50% of the fish, and courting and spawning occurred in each group. Thus, fish appeared to respond favourably to laboratory conditions.

Individual fish demonstrated territorial behaviour throughout the entire experimental period, and their use of territories occupied during the spawning season continued after the end of the reproductive season. Defence of space within the same area of the pool throughout the six-month period suggests that space use may be consistent throughout the entire year.

Of 27 individuals used, only two fish died.

Distribution of territories

General observations showed that the most dominant fish in a group usually controlled up to 35% of the bottom area available. Considerable overlap existed between defended areas and access to areas of overlap was dominance-related. The more dominant fish of the overlapping pair used this area without dispute, whereas the more subordinate individual had access to and defended this area only when the dominant was elsewhere. Therefore, defended areas of some adjacent conspecifics overlapped in space but not in time. However, defence of the overlapped area by the subordinate against less dominant individuals was as vigorous as defence of the remainder of its territory. In each pool, a small number of fish defended areas that shifted from day to day. Sometimes these same fish defended no area, but took cover in peripheral rock rubble and remained there for days at a time. These fish were usually small and always subordinate.

A linear regression showed that the proportion of entire territory that was overlapped, was inversely correlated with dominance rank (Table 3). Territories of subordinate fish had proportionately greater overlap than did territories of more dominant fish.

In some cases, the territory of a subordinate overlapped the territories of more than one dominant fish. When displaced by one aggressive dominant, the subordinate simply moved to a new position in the adjacent dominant's territory. When not being displaced by either of the two dominants, the subordinate continued to defend its borders and exclude fish less dominant than itself. When displaced entirely from its territory, the subordinate generally retreated to the rock rubble at the perimeter of the pool, and remained out of sight for a short period of time. In this way, a subordinate could escape continuous harrassment by aggressive dominants.

The resulting pattern of space use is one of a territorial mosaic among dominant fish, with smaller fish defending some of the same area against more subordinate individuals, in the absence of resident dominants.

Characteristics associated with space defence

Linear dominance hierarchies were rapidly established, and dominance within groups did not change over the experimental period, prior to the removal of the alpha fish. There was a strong correlation between size rank and dominance rank of individuals ($r=0.89$, $p<0.0001$. Fig.2).

The entire area of territory of individual fish was strongly affected by dominance rank, but not by group ($p<0.001$, two-way ANOVA). In all three pools, the alpha fish controlled the largest area of territory, and a decreasing area of entire territory was correlated with increasing subordinance (Table 4).

The size of the exclusive portion of territory was also significantly affected by dominance rank ($p<0.001$, two-way ANOVA) but not by pools ($p>0.05$). Again, in all three pools the most dominant fish controlled the largest exclusive area, and decreased size of the exclusive area defended was associated with increasing subordinance (Table 4).

In two of the three groups, when the most dominant fish was removed, the beta fish became the new alpha; one of these new alphas was female (Table 5). In the third group (Pool 1), after alpha removal the female beta fish dropped to fourth rank. This was the only loss of rank recorded; all other rank changes involved an increase in dominance. Associated with an increase in dominance was a corresponding increase in the entire area of territory (p=.001, Wilcoxon two-sample test. Table 5). However, the new alpha did not neccessarily have the largest territory. Although the removal of the alpha fish resulted in fewer fish per pool, the subsequent increase in territory size of remaining fish may not have been due only to reduced population density, since prior to the removal of the dominant approximately 25 per cent of the substrate was undefended.

In all groups, females successfully held and defended territories. In no case was a female the most dominant fish in the group (prior to the removal of the alpha fish), but no female was initially the largest fish in its group. The area of territories held by females was similar to that of similar-ranked males in other groups (Table 5).

Experiment 2

General

In both groups (A and B), established in late September, territories were rapidly established and vigourously defended by both females and males. In most cases, territories were at the same location when individuals were removed 10 months later. For males, such territories were often the site for courting behaviour and egg-guarding during the reproductive season.

The mortality in Exp.2 was higher than that of Exp.1. Of 42 fish, 6 were dead by early March when the reproductive season started. By late June, another 15 were dead (Table 6). Thirteen of seventeen low-ranking fish that died were female; the remaining mortalities were high-ranking males. One of those developed a necrotic abscess in the shoulder region and subsequently died. However, the other three males appeared healthy, and all had successfully hatched eggs within the previous month.

Distribution of territories

Territories of dominant fish were large, and did not overlap extensively with those of other high-ranking fish. However, superimposed upon the territories of dominant fish were smaller territories of individuals of more subordinate status (Fig.3). Often, territories among subordinates were also mutually exclusive, but overlapped to a large extent with those of more dominant fish. The degree of overlap was not correlated with dominance rank in Group A or B during the non-reproductive or the reproductive season (Table 7). In Group C, established just prior to the reproductive season, however, there was a strong correlation between overlap and dominance rank.

As in Exp.1, access to areas of overlap was dominance-related, and some subordinate fish frequently overlapped more than one dominant's territory. However, occupation and defence of these overlapping areas by subordinate fish was conditional upon the absence of the co-resident dominant. But unlike conditions in Exp.1, subordinates did not have access to retreat that offered visual or physical escape from dominants. Such fish were often displaced from territory to territory of dominant fish, until a temporary hiding spot could be found. Some subordinates were unable to establish territories at all and moved continually from one area to another in an attempt to avoid aggressive behaviour by territorial fish.

Characteristics associated with space defence

The size rank and dominance rank of each fish in groups A, B and C were plotted shortly after the start of the experiment, and again after the start of the reproductive season. Linear regressions show that size rank and dominance rank were significantly correlated (Table 8). In a few cases, high-ranking dominants were female but most of the subordinate fish in each group were also female. As most females were also the smallest fish in each group, this may be a reflection of their sex-size distribution rather than a sex-related effect.

Correlations between the entire territory size and the dominance rank of fish within groups were high in Group B and Group C (Table 9) during both the reproductive and non-reproductive seasons; as subordinance rank increased, area of territory decreased. Group A, however, showed no such correlation. Correlations between the exclusive area of territory and dominance rank in fish of Group A were low during both the reproductive and non-reproductive season (Table 10). as was the case with fish in Group B during the non-reproductive season. However, Groups B and C, during the reproductive seasons showed a significant correlation; the area of exclusive territory decreased as subordinance rank increased.

Effect of season on territory area

Close to half of the territorial fish in Groups A and B showed a significant increase in exclusive, or the entire are of territory, or both, in the reproductive season compared to the previous non-reproductive season

(Table 11 and 12). These increases were not consistently correlated with the degree of spawning success, nor were they consistently associated with an increase in dominance rank. An increase in the number of structures providing cover was often, but not always, concomitant with an increase in territory area.

Five of thirteen territorial fish examined showed an increase in aggression during the reproductive season. In three of five fish, this was associated with an increase in either the entire or the exclusive area of territory, or both (Table 11 and 12). Of these same fish, three showed an increase in dominance rank from the non-reproductive to the reproductive season, one showed a loss of dominance rank, and one retained its original rank.

Effect of presence of eggs on territory size

In only two of nine cases was the entire area of territory affected by the presence of eggs (Table 13, 14 and 15); in both cases, territory size increased. Otherwise, little disruption of the overall distribution of territories resulted. However, in seven of nine cases, the exclusive area (i.e. unshared by conspecifics) was significantly increased with the presence of eggs. During the reproductive season, territories appeared to have stable outer boundaries, with elastic central areas from which all conspecifics were always excluded, and the size of the central area was dependent upon the presence or absence of eggs. The number of chases was generally unaffected by the presence of eggs, except for two individuals, where aggressive activity significantly increased.

E. Discussion

General

Populations of fish from both experiments demonstrated long-term territoriality and strong site-fidelity. This supports field observations that individual *C. nicholsi* demonstrate long-term territorial behaviour.

Mortality in Exp.2 was much higher during the reproductive season than prior to this time. Many of the deaths were those of subordinate females. This suggests that there is a heavy cost associated with low dominance rank, the production of eggs, or both. Since most subordinate fish were female, however, conclusions about the relative effects fo these two factors cannot be made. In Exp.1, where mortality was very low, the reproductive season was over approximately eight weeks after the groups were established, and there was only one recorded spawning event in each pool during this time. In addition, many hiding spots were available in the perimeter of rock rubble. In contrast, groups of fish in Exp.2 had no such additional cover available, and were maintained for the entire reproductive season (approximately 20 weeks). Little is known about the cost of egg production in fish, but it is an energetically demanding period for mature individuals, and may be a factor in female mortality.

The deaths of three large, apparently healthy male fish are unexplained. All had just recently hatched eggs, and their condition appeared good. Parental activity including defence behaviour may place considerable stress on males, and be a factor in male mortality during the reproductive season.

Distribution of territories

The pattern of spatial partitioning found in these experimental groups matches that found in field populations (see Paper 1). Dominant (i.e., large) fish were spaced out and controlled a large portion of the available substrate area. Superimposed upon this were territories of less dominant (i.e., smaller) fish. However, unlike the field situation, the subordinate fish in the experimental pools rarely had an exclusive area of territory with an unshared retreat. In these groups, the artificial pool boundaries prevented escape of subordinates. In addition, rock rubble cover that is abundant in the field was scant (Exp.1) or absent (Exp.2). Hence, subordinates were rarely out of sight of dominants and some had difficulty establishing territories. The ability of smaller *C. nicholsi* to exist alongside large, presumably dominant fish in field populations, at high densities, may be directly related to the greater degree of topographical heterogeneity present in their natural habitat.

The pattern of space use demonstrated by *C. nicholsi* and typified by conditional territorial exclusion based on relative dominance rank of intruders, appears similar to that found in juvenile sunfish, *Lepomis cyanellus*. Greenberg (1947) described these as "partial territories"; he considered such territories intermediate between a dominance hierarchy and a territory. Similarly, Newman (1956) felt that dominance-subordination relationships showed a level of aggression intermediate to the low levels required for schooling, and the high level necessary for territoriality. This attitude reflects a more restricted view of territory, as a completely exclusive area. I feel that the conditional territories defended by subordinates and described here are true territories, but with different characteristics of defence than those of classically exclusive areas such as breeding territories. The pattern of space partitioning characterized by spatial but not temporal overlap of defended areas may be more typical of long-term territories, particularly in populations of mixed sex and mixed size.

Characteristics associated with space defence

The presence of dominance effects within the territorial organization of laboratory populations has been clearly shown. Dominance hierarchies in *C. nicholsi* are of the "nip-dominant" type (Myrberg 1972), as opposed to a "nip-right" type (Braddock 1945) where subordinate fish never challenge dominants. The outcome of any one interaction between two fish was not automatically in favour of the dominant, and changes in dominance ranks of individuals did occur over the experimental period.

The presence of dominance hierarchies in laboratory populations supports the apparent presence of dominance hierarchies in natural populations (see Paper 1). However, while dominance behaviour is common among fish in captivity, clear evidence for it in natural populations of fishes is limited (Keenleyside 1979). In the bicolor damselfish, *Eupomacentrus partitus*, a species with territorial males and associated females, there is a strong hierarchical structure within females in both laboratory and field colonies (Myrberg 1972). Other reports of dominance hierarchies in territorial fish also often involve haremic situations (Ross 1978, Fricke 1980).

Laboratory populations of *C. nicholsi* have patterns of space partitioning, invasive behaviour of overlapping territories, and defence determined by invader size similar to that of field populations. Hence the inference is strong that dominance relationships play as important a role in the social organization of field populations of this species as that found in laboratory populations.

In laboratory populations, there is a strong direct correlation between fish size rank and dominance rank. Size has frequently been found to be a determinant of dominance in other fish (Noble 1939, Greenberg 1947, Newman 1956, Chapman 1962, Myrberg 1972). This relationship may be responsible for the common pattern of space partitioning found in mixed-age and mixed-size populations where smaller fish exist interstitially or peripherally to territories of larger fish, and considerable overlap in space use occurs (Keenleyside 1972, Barlow 1975, Nursall 1977, Moran and Sale

1977). Differences in the amount of in overlap between territories may reflect variation in dominance relationships between adjacent conspecifics.

Dominance rank and the size of territory were also strongly correlated in most laboratory groups. Hence, through dominance, large fish controlled much of the available substrate. Smaller fish used interstitial areas undefended by larger fish, and defended other area conditionally in the absence of an overlapping dominant. That larger dominant fish defended larger territories than smaller fish may explain the inverse correlation found between dominance rank and degree of overlap. The actual amounts of overlap may be the same between size classes, but represent differing portions of entire area of territory, depending upon its territory size.

Increases in dominance rank also brought an attendent increase in territory size. The subsequent expansion of territory sizes following the removal of the alpha may indicate inhibition of space use by dominants over subordinates, and a concomitant increase in access to space with increased dominance rank. As dominant fish determine the movements of subordinate fish, the control of space appears to be behaviourally regulated by direct aggression and dominance effects.

In laboratory populations, the sex of similar-sized individuals did not appear to affect their ability to defend space, as shown by high-ranking females. However, within age classes, females of this species tend to be slightly smaller (1-4 mm SL) than males (Wiley 1973). The findings in these experiments suggest that such a difference is often sufficient to generate dominance differences. This may mean that females tend to be at a permanent disadvantage to males of the same age class in their ability to acquire and defend a territory.

Effects of season and reproduction on territory size

The general increase of territory area associated with the reproductive season by high-ranking dominants differs with findings in the field, where no effect of season was found (see Paper 1). However, in the field, areas of all large individuals were grouped to look for seasonal effects on territory size, irrespective of sex, dominance, or spawning success (none of which were known). Hence, changes in territory areas of successful spawning males may occur in natural populations much as they did in laboratory groups.

Having a larger territory during the reproductive season provides a larger area in which to carry out courting displays. Courting behaviour by males involves conspicuous movements including fin extention and exaggerated body undulations while swimming to and along the territory border (see Paper 4). A larger territory border provides a larger display path, and visual access to a greater number of females. Since males do not leave their territories to seek females, an increased display perimeter may increase reproductive success.

Within the reproductive season, the entire territory area of individual fish appeared to remain constant over time, but an increased size of the exclusive area was strongly correlated with the presence of eggs. A larger exclusive area during egg-guarding may reflect an attempt to reduce egg predation by both conspecifics and heterospecifics (see Paper 4).

The importance of dominance in the territorial system of *Coryphopterus nicholsi* cannot be overemphasized. Dominance rank is a measure of an individual's freedom of access to limited resources, in this case, space. Indeed, all factors involved in dominance are also important in the establishment of a territory (Greenberg 1947). The findings of these experiments indicate that territorial social systems are extremely dynamic on the individual level, with complex inter-relationships between season, size and dominance of the territory holder, as well as the parental state of males during the reproductive season. Extrapolations to field populations must be done with care. However, laboratory studies on *C. nicholsi* suggest that upon more detailed field studies, such factors may be found to be of major importance in understanding the territorial social structure of this species.

F. Acknowledgments

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Table 1. Standard length (mm) and sex of fish used in each of three groups in Experiment 1. M is male; F is female

GROUP 1		GROUP 2		GROUP 3	
M	82.6	M	85.3	M	85.0
F	81.1	M	84.7	M	82.4
M	80.0	M	73.6	F	74.7
F	69.2	M	69.8	M	73.5
M	67.0	F	64.9	F	67.5
F	60.3	F	60.7	F	65.7
M	57.8	M	60.4	M	63.0
F	57.2	F	58.4	F	62.4
F	50.5	F	50.7	F	51.3

Table 2. Standard length (mm) and sex of fish used in each of three groups in Experiment 2. M is male; F is female

GROUP A		GROUP B		GROUP C	
F	81.8	F	85.4	M	90.1
M	81.6	M	84.6	M	86.4
M	78.2	F	82.4	M	86.2
M	78.0	F	82.0	M	84.3
F	77.8	M	76.0	M	84.2
F	76.8	M	74.5	M	83.2
F	76.4	F	73.2	M	80.4
M	75.3	F	72.4	F	78.0
M	74.8	M	70.3	F	75.3
F	74.3	F	70.2	F	75.1
F	74.3	F	66.8	F	73.1
M	74.1	M	66.1	F	70.8
F	73.8	F	65.3	F	67.2
M	73.2	M	64.0	F	60.5

Table 3. Mean overlap as percentage of total territory area for individual fish in Pools 1, 2 and 3, in Experiment 1 prior to removal of alpha. Column headings indicate dominance rank; 1 is most dominant and 4 is least dominant. The mean value (m), standard deviation (SD) and number of observations (n) are given for each fish in each group. M is male; F is female. r value is based on linear regression

		DOMINANCE RANK			
		1	2	3	4
		M	F	M	F
POOL 1	m	32.3	51.3	37.0	54.2
	SD	23.6	38.4	29.6	35.7
	n	6	6	4	6
		M	M	M	F
POOL 2	m	17.8	16.5	30.4	54.2
	SD	14.6	11.3	17.7	39.1
	n	9	6	8	6
		M	F	F	
POOL 3	m	7.7	9.7	5.6	
	SD	6.8	13.4	9.8	
	n	3	3	3	

r=0.68 p=0.03

Table 4. Area of territory (m^2) for entire area, and area of exclusive portion of territory defended by fish of different dominance ranks prior to alpha removal, in Experiment 1. 1 is most dominant and 4 is least dominant. r values are based on linear regressions

a) Area of entire territory vs dominance

	Dominance Rank			
	1	2	3	4
POOL 1	.51	.22	.11	.13
POOL 2	.36	.19	.16	.05
POOL 3	.32	.21	.07	0

$r=-0.87$ $p=0.0001$

b) Area of exclusive portion of territory vs dominance

	Dominance Rank			
	1	2	3	4
POOL 1	.32	.11	.06	.05
POOL 2	.30	.16	.10	.03
POOL 3	.29	.19	.06	0

$r=-0.94$ $p=0.00001$

Table 5. Change in mean size of entire territory associated with change in dominance rank in Experiment 1. Initial indicates dominance rank and mean size of entire area of territory of individual fish, prior to alpha fish removal. Final indicates new dominance rank and mean size of entire area of territory of the same fish, after removal of the alpha fish. 1 is most dominant; 4 is least dominant. A is area of territory; SD is standard deviation; N is number of observations when fish were active and territory area could be determined. * indicates female fish

	Dominance Rank							
	Pool 1			Pool 2			Pool 3	
Initial	2*	3	4*	2	3	4*	2*	3*
A	.22	.11	.13	.19	.16	.05	.21	.07
SD	.12	.07	.08	.08	.06	.02	.05	.01
N	6	4	6	6	8	7	3	3
	Pool 1			Pool 2			Pool 3	
Final	4*	1	2*	1	2	3*	1*	2*
A	0	.25	.29	.26	.34	.17	.54	.18
SD		.13	.13	.10	.11	.14	.12	.11
N	2	12	11	9	9	9	13	13

Table 6. Fish mortality in Groups A, B and C of Experiment 2. Dates at column headings indicate time period during which mortalities occurred. M is male; F is female. Values following indicated sex are standard length (mm). Numbers in brackets indicate dominance rank at time of death; 1 is highest and 13 is lowest; fractional numbers indicate codominance with another fish in the group

Group A	By Mar.4	By Apr.14	By May24	By June19
	F 74 (12.5)	F 79 (9.5)	M 90 (1)	M 88 (3)
		M 73 (8.5)	M 87 (2)	
		F 80 (13)		

Group B	By Feb.8	By Mar.6	By June4	By June25
	M 63 (11.5)	F 70 (8)	F 66 (9)	M 85 (4)
	M 70 (11.5)			F 73 (8)
	M 76 (11.5)			
	F 85 (11.5)			

Group C	By Feb.16	By Apr.28	By June26
	F 60 (14)	F 80 (9)	F 67 (7.5)
			F 70 (11)
			F 73 (9)
			F 75 (10)

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Table 7. Mean proportion of entire territory shared for a)non-reproductive and b)reproductive seasons. Numbers at column headings indicate dominance rank just prior to the reproductive season; 1 is most dominant; 10 is least dominant. Where fish have equal dominance rank, both values for proportional overlap are listed under the appropriate dominance rank. r values are based on linear regressions of dominance to proportion of shared territory. Individuals showing little or no territory defence are not included

a) Non-reproductive season

	Dominance Rank							
	1	2	3	4	5	6	7	
Group A	.25	.23	.44 .13		.42	.38		r=0.54 p=0.27
Group B	.39	.56	.39	.03	.40 .51		.16	r=-0.34 p=0.45

b) Reproductive season

	Dominance Rank							
	1	2	3	4	5	6	7	
Group A	.50 .11		.19 .10		.42	.51		r=0.39 p=0.44
Group B	.26	.34	.54 .35		.35 .46		.53	r=0.66 p=0.10

	Dominance Rank						
	1	2	3.5	5	7.5	10	
Group C	.37	.40	.41 .40	.59	.65	.88	r=0.96 p=0.0005

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Table 8. Size rank (standard length) and dominance rank of fish in Groups A, B and C in Experiment 2. Ranks were assessed in October and the following March for Groups A and B, and in March for Group C. D represents dominance rank; 1 is most dominant and 13 is least dominant. S indicates size rank; 1 is largest and 14 is smallest. In cases of equal size or dominance rank, individuals are both assigned an intermediate value. r values are calculated by linear regression. * indicates female

Group A				Group B				Group C	
October		March		October		March		March	
D	S	D	S	D	S	D	S	D	S
1	1.5	1.5	1	1	1	1	1	1	1
*2	1.5	1.5	5	2	2.5	*2	2	2	4.5
3.5	4	3.5	2.5	*3	2.5	3.5	3	3.5	4.5
*3.5	7	3.5	4	4	4	3.5	4	3.5	7
5	4	5	2.5	*5.5	5	*5.5	5.5	5	2.5
6	8.5	6	8.5	*5.5	6	*5.5	5.5	6	2.5
7	8.5	*7	6	*7	7	*7	7	*7.5	9.5
*8	4	8	10	8	9.5	8	9	*7.5	13
*9	11.5	*9.5	7	*9.5	8	*9.5	8	*9	11
*10	6	*9.5	11	*9.5	9.5	*9.5	10	*10	9.5
*12.5	14	*11	12					*11	12
*12.5	11.5	12	8.5					*12	8
12.5	11.5	*13	13					13	6
12.5	11.5								
r=0.85 p=0.0001		r=0.85 p=0.0002		r=0.97 p=0.0001		r=0.98 p=0.0001		r=0.61 p=0.03	

Table 9. Entire area of territory (m^2) for fish of different dominance ranks, for a) non-reproductive and b) reproductive seasons, in Groups A, B and C of Experiment 2. Column headings indicate dominance rank at the beginning of each season; 1 is most dominant and 10 is least dominant. Where fish have equal dominance rank, both values for area of territory are listed under the appropriate rank. Individuals showing little or no territorial defence are not included. r and p values are based on linear regressions

a) Non-reproductive season

	Dominance Rank											
	1	2	3		4	5		6	7	8		
Group A	.64	.23		.22		.18		.17	.13		r=-0.78	p=0.07
Group B	.42	.30	.26		.21		.27		.17	.13	r=-0.87	p=0.01

b) Reproductive season

	Dominance Rank													
	1		2	3		4	5		6	7		8		10
Group A		.49 .55			.31 .33		.43		.39				r=-0.55	p=0.26
Group B	.70		.55		.32 .37			.26 .24				.21	r=-0.90	p=0.006
Group C	.78		.58		.60 .45		.26				.36		r=-0.87	.20 p=0.01

Table 10. Exclusive area of territory (m^2) for fish of different dominance ranks, for a) non-reproductive and b) reproductive seasons, in Groups A, B and C of Experiment 2. Column headings indicate dominance rank at the beginning of each season; 1 is most dominant and 10 is least dominant. Where fish have equal dominance rank, both values for area of territory are listed under the appropriate rank. Individuals showing little or no territorial defence are not included. r and p values are based on linear regressions

a) Non-reproductive season

	Dominance Rank								
	1	2	3	4	5	6	7	8 ✓	
Group A	.49	.13	.17		.10	.10	.12	r=-0.71	p=0.11
Group B	.19	.20	.11	.20	.16		.10	.10 r=-0.71	p=0.07

b) Reproductive season

	Dominance Rank								
	1	2	3	4	5	6	7	8	10
Group A	.24 .48		.26 .29		.26	.22		r=-0.58	p=0.23
Group B	.43	.36	.23 .13		.16 .11			.09 r=-0.87	p=0.01
Group C	.43	.34	.35 .27		.12		.11	r=-0.94	.03 p=0.002

Table 11. Effect of season on the mean area of entire and exclusive portion of territory, the mean number of cover defended, and the number of chases per minute initiated by fish in Group A, Experiment 2. N is non-reproductive season and R is reproductive season. Fish are ordered by decreasing dominance determined at the beginning of the experiment, from left to right. M is male; M_F is male recently changed from female. Numbers at the top of the columns indicate initial standard length (mm) at the beginning of the experiment, and standard length at the beginning of the reproductive season in March. and - following March standard length of each fish indicate an increase or decrease, respectively, in dominance rank from the beginning of the experiment to the beginning of the reproductive season. Area of territory is m^2; mean values are based on 8 observations during non-reproductive season and 23 observations during reproductive season. The bottom row indicates the total number of egg masses acquired over the experimental period. Asterisks indicate significant differences (p 0.05) between non-reproductive and reproductive season values (t-test)

		M	M_F	M	M	M	M
Initial SL		81.6	81.8	77.8	74.8	78.0	75.3
March SL		87.5^-	86.7^-	86.0^+	87.0^+	86.7	81.0
Entire Area	N	.64	.23	.22	.13	.18	.17
				*	*	*	*
	R	.49	.31	.55	.33	.43	.39
Exclusive Area	N	.49	.13	.17	.12	.10	.10
		*	*	*	*	*	
	R	.24	.26	.48	.29	.26	.22
Total No. of Cover	N	3.8	1.9	1.4	0.9	0.9	0.8
				*	*	*	*
	R	2.6	2.1	3.6	1.7	2.3	1.9
Exclusive No. of Cover	N	2.4	1.1	1.3	0.4	0.4	0.4
		*		*	*		
	R	1.1	1.5	2.9	1.5	1.0	0.9
Number of Chases	N	.33	.12	.10	.08	.11	.09
				*	*	*	
	R	.21	.11	.19	.18	.33	.19
Number of Egg Masses		1	1	4	1	0	1

Table 12. Effect of season on the mean area of the entire and the exclusive portion of territory, the mean number of cover defended, and the number of chases per minute initiated by fish in Group B, Experiment 2. N is non-reproductive season and R is reproductive season. Fish are ordered from left to right by decreasing dominance, determined at the beginning of the experiment. M is male; M^F is male recently changed from female; F is female. Numbers at the top of the columns indicate initial standard length (mm) at the beginning of the experiment, and standard length at the beginning of the reproductive season in March. and - following March standard length of each fish indicate an increase or decrease, respectively, in dominance rank from the beginning of the experiment to the beginning of the reproductive season. Area of territory is m^2; mean values are based on 8 observations during non-reproductive season and 23 observations during reproductive season. The bottom row indicates the total number of egg masses acquired over the experimental period. Asterisks indicate significant differences (p 0.05) between non-reproductive and reproductive season values (t-test)

		M	M_F	M	M	F	F	M
Initial SL		84.6	85.4	74.5	82.0	72.4	73.2	66.1
March SL		91.2	88.4$^+$	85.7$^+$	87.1$^-$	77.1$^+$	77.4	73.0
Entire Area	N	.42	.26	.21	.30	.17	.27	.13
			*			*		
	R	.70	.55	.32	.37	.26	.24	.21
Exclusive Area	N	.19	.11	.20	.20	.10	.16	.10
		*	*					
	R	.43	.36	.23	.13	.16	.11	.09
Total No. of Cover	N	3.5	1.6	1.5	2.1	2.1	1.5	0.5
								*
	R	3.9	2.5	2.1	2.5	1.8	1.7	1.6
Exclusive No. of Cover	N	1.1	0.5	1.3	0.8	0.9	0.3	0.3
			*					
	R	2.3	1.3	1.1	0.7	0.6	0.6	0.5
Number of Chases	N	.17	.11	.04	.12	.07	.11	.04
				*	*			
	R	.14	.17	.15	.22	.11	.11	.08
Number of Egg Masses		5	3	1	0			0

Table 13. Mean values for the area of territory (m^2) and and number of chases initiated per minute by fish in Group A, Experiment 2, during periods with spawn (S) and without spawn (NS). M is male; M_F is male recently changed from female. Fish are ordered by decreasing dominance from left to right. The bottom row indicates the total number of egg masses acquired during the experimental period. ● indicates an insufficient number of observations either with eggs or without eggs, to make a comparison. Asterisks indicate significant differences between values for periods with eggs and without eggs ($p<0.05$, t-test)

		M	M	M_F	M	M
Entire Area	S	●	.50	.32	.34	●
	NS		.63	.21	.25	
Exclusive Area	S		.44	.32 *	.36 *	
	NS		.53	.16	.20	
Number of Chases	S		.20	.07	.18	
	NS		.16	.13	.20	
Number of Egg Masses		1	4	1	1	1

Table 14. Mean values for the area of territory (m^2) and number of chases initiated per minute by fish in Group B, Experiment 2, during periods with spawn (S) and without spawn (NS). M is male; M_F is male recently changed from female. Fish are ordered by decreasing dominance from left to right. The bottom row indicates the total number of egg masses acquired during the experimental period. ● indicates an insufficient number of observations either with eggs or without eggs, to make a comparison. Asterisks indicate significant differences between values for periods with eggs and without eggs ($p<0.05$, t-test)

		M	M_F	M
Entire Area	S	●	.50	.66
				*
	NS		.37	.20
Exclusive Area	S		.41	.62
			*	*
	NS		.12	.16
Number of Chases	S		.11	.21
				*
	NS		.12	.09
Number of Egg Masses		5	3	1

Table 15. Mean values for the area of territory (m^2) and number of chases initiated per minute by fish in Group C, Experiment 2, during periods with spawn (S) and without spawn (NS). M is male. Fish are ordered by decreasing dominance from left to right. The bottom row indicates the total number of egg masses acquired during the experimental period. ● indicates an insufficient number of observations either with or without eggs, to make a comparison. Asterisks indicate significant differences between values for periods with eggs and without eggs ($p<0.05$, t-test)

		M	M	M	M	M
Entire Area	S	.82	.70	.59	●	.38
						*
	NS	.69	.57	.58		.24
Exclusive Area	S	.50	.67	.51		.30
			*	*		*
	NS	.42	.30	.30		.06
Number of Chases	S	.44	.39	.30		.23
		*				
	NS	.21	.38	.45		.14
Number of Egg Masses		3	2	2	1	1

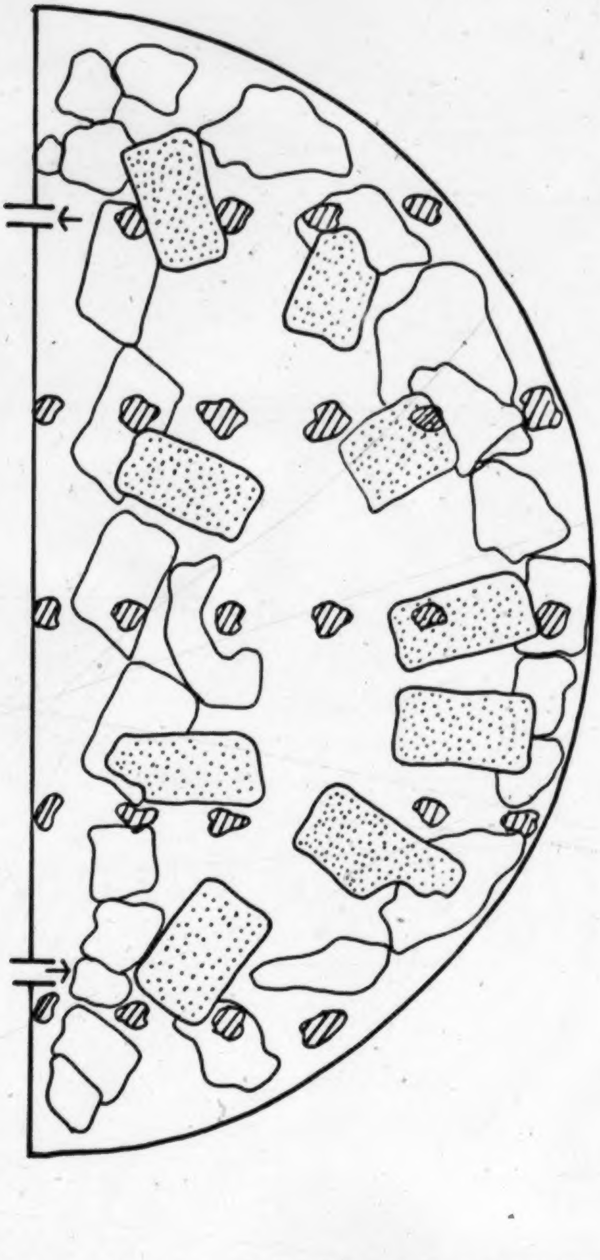

Figure 1. Illustration of substrate topography of one of the pools in Experiment 1. Clear shapes indicate rocks used for perimeter border; stippled shapes represent bricks propped up on rocks to provide cover; hatched shapes show small stones used to mark a bottom grid at 0.2 m intervals. Arrows show the direction of water flow.

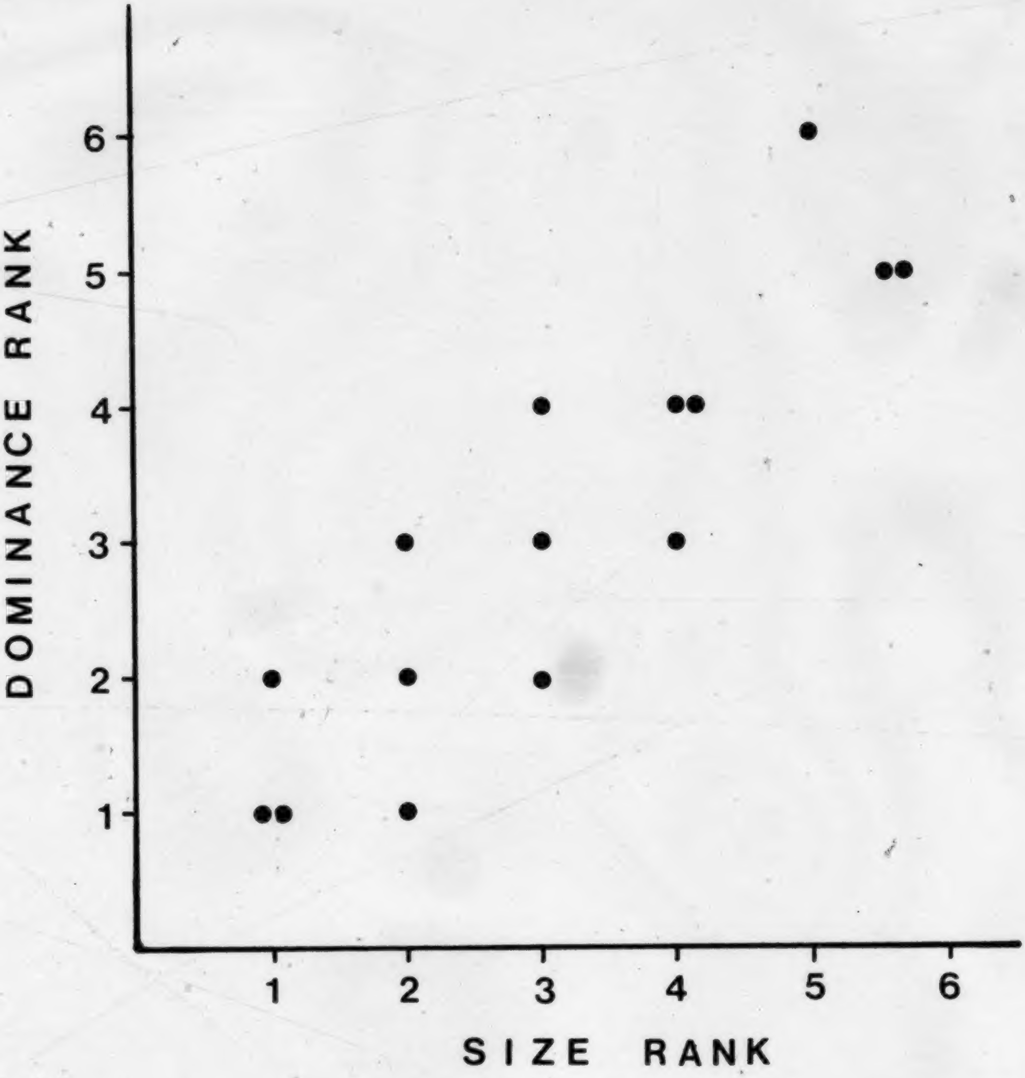

Figure 2. Dominance rank versus size rank for fish in Experiment 1. For size rank, 1 is largest and 6 is smallest. For dominance rank, 1 is most dominant and 6 is least dominant

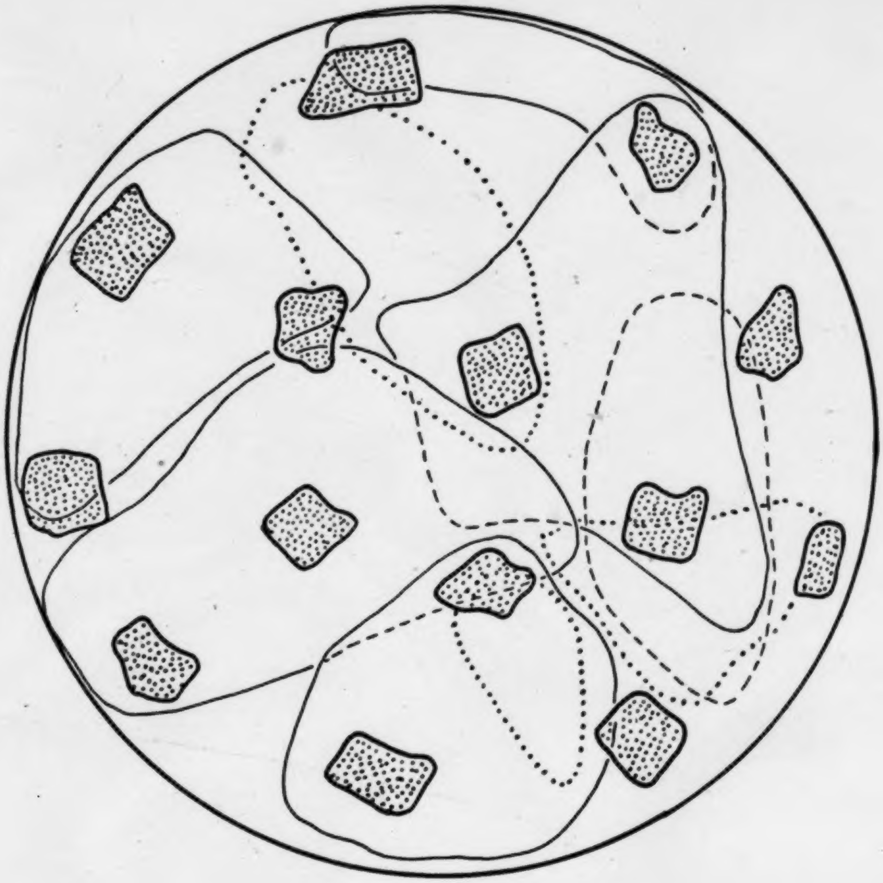

Figure 3. Territory map showing overlapping of territories in Experiment 2. Stippled shapes represent units of cover. Solid lines indicate territory boundaries of dominant fish; dashed lines indicate territory borders within boundaries of more dominant individuals. Dotted lines show territories of most subordinate fish defending space. Border locations were determined over one observation period.

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III. Paper 3. Protogynous Hermaphroditism in a Temperate Zone Territorial Marine Goby, *Coryphopterus nicholsi*

A. Abstract

Coryphopterus nicholsi is a temperate zone Pacific goby. Fish in laboratory populations demonstrated the ability to change sex from female to male (protogynous hermaphroditism). Intersexual fish collected from the field indicate that this process occurs in natural populations. There are two females for every male in the population; most small fish are female and most large fish are male. Changes in gonad structure consisted of the development of spermatic tissue along the periphery of the old ovarian lumen. This was accompanied by degeneration of ovarian tissue. Secondary testes had multiple lumina for the retention and transport of sperm. All testes examined in the population showed the same structure, suggesting that this species may be monandric. Social cues are important in initiating sex change, but other factors, as yet unknown, also appear to play a role.

B. Introduction

Sex change among marine fishes has been documented for many families (Atz, 1964; Choat and Robertson, 1975; Reinboth, 1975; Warner and Robertson, 1978; Jones, 1980; Shapiro, 1981). I am aware of only two papers on confirmed hermaphroditism in the family Gobiidae, including four pair or group-living *Paragobiodon* spp. from the western Pacific (Lassig, 1977), the schooling *Coryphopterus personatus*, and solitary *Gobiosoma multifasciatum* from the Caribbean (Robertson and Justines, 1982).

C. nicholsi is a small (maximum 100 mm standard length), benthic goby that inhabits rock rubble areas in protected shallow waters along the west coast of North America (Hart, 1973). Externally, the only evidence for sexual identity is the shape of the genital papilla, which is elongate in males and short and broad in females (Wiley, 1973). In the course of laboratory behavioural studies at Bamfield Marine Station, Bamfield, British Columbia (latitude 49 N, longitude 125 W), evidence was found for the occurrence of protogynous sex change in this species.

C. Methods and Materials

Experimental fish were captured with the use of minnow traps and their sex determined on the basis of papilla structure. Of these fish, some were killed immediately and gonadectomized, and the rest were given a subcutaneous dye mark indicating assigned sex and maintained in laboratory groups.

In September 1979, a census was carried out on a holding pool containing over 30 *C. nicholsi* of both sexes, and on three experimental populations, each of 7 to 14 males and females that were established for one month in August 1979. Dye marks of individuals, indicating initial assigned sex were compared with present papilla structure. Where changes in papilla structure had occurred, the identity, and where possible, the size rank of the individual were recorded.

In late September 1979, two laboratory groups of 14 fish (7 females and 7 males in each, Groups A and B) were established, and re-checked in January 1980 for changes in the shape of the genital papilla associated with sex change. A third laboratory group of 7 females and 7 males (Group C), was set up in February 1980. All three pools were censused in March and again in July 1980. Following this, the fish were killed. The gonads were removed, placed in Bouin's solution, sectioned serially at 7 microns, and stained with Harris' haemotoxylin/precipitated alcoholic eosin.

In addition, a pool of 16 females was set up in January 1980, and examined monthly until July 1980 for signs of sex change, based on change in papilla form. At this time, all fish in the pool were killed, and their gonads examined histologically. A second all-female population of 19 fish was established in July 1980. No interim observations were made on this population, but five months later, all the individuals were killed and the gonads sectioned and examined.

D. Results and Discussion

In over two hundred gonadectomized fish examined over a three year period, there was complete correlation between the form of the genital papilla and the gonad type (ovary or testes), indicating that sex of individuals can be determined reliably from papilla structure.

In Groups A and B, five months after establishment in September 1979, three of the fourteen fish originally designated female had typical male genital papillae, and another two had short but pointed papillae that appeared to be transitional. By late March, eight weeks later, the latter two fish had fully developed male papillae. All transforming females were either the largest or second largest female in their group at the time of sex change (69 mm to 82 mm SL). However, larger males were present when females changed sex.

Between March and July 1980, the first three fish in Groups A and B noted to change sex actively courted females, obtained spawn, and guarded eggs through to hatching, indicating a successful transition to male. The other two fish that changed sex were not observed courting females or guarding eggs that summer. Histological examination of the gonads of all fish originally designated female in these groups, at the end of the reproductive season, confirmed testicular development in the five transformed males; the gonads of the remaining females were entirely ovarian. In Group C, no sex changes occurred.

Five instances of sex reversal were discovered in other mixed-sex groups of fish. Three transformed fish were discovered in September 1979 in groups of 7 to 14 fish; each was the largest female in its group (75 to 85 mm SL), but larger males were present at the time of sex change. Two fish from a general holding pool, censused at that time, were also transformed. Their size relative to other fish at the time of sex change was unknown.

In the group of 16 females established in January 1980, all still had typically female genital papillae by April 1980. However, by the end of May, the second-largest fish had a typical male genital papilla, and by mid-July, four more fish had become male (size ranks of transformed fish were 2, 5, 8, 11, and 15).

In the all-female population of 19 fish, histological examination of all fish after five months showed eight females to have developing or fully-formed testes (size ranks of transformed males, based on initial size, were 2, 3, 4, 5, 6, 8, 12, and 13). Because no interim observations were made in this group, the time at which individual sex change occurred is unknown.

In 1980, four fish having short, pointed papillae were collected from field populations. The time of collection and standard length of fish were: January, 67 mm and 84 mm; April, 77 mm; May, 88 mm. When their gonads were examined histologically, all were found to be sexually transitional.

In a histological survey of gonadal tissue, based on approximately 40 females, 35 males and 20 transitional specimens, the following structural patterns were found.

In an ovary, the egg-bearing cortex projected into a central lumen; no spermatic tissue was evident (Fig.1a). In early stages of transitional gonads (ovotestes) examined, various ovarian features were still present, including a thick cortex (the old ovarian wall), oocytes, and large follicles containing yolk. In addition, small nests of spermatic cells were present, adjacent to the lumen (Fig.1b). The lumen was usually considerably reduced, and much of the remaining tissue was unstructured, and characterized by macrophage activity. In progressively transformed ovotestes, oocytes and yolky deposits were generally absent, and large discrete areas of undifferentiated tissue formed the periphery of the gonad. Throughout the length of the gonad, well-developed medullary spermatic tissue lined the old ovarian lumen (Fig.1c). New lumina may have resulted from the formation of tubules of spermatic tissue, and at this stage, sperm were frequently present. In late stage transitional testes, the lumen consisted of branched and anastomosing channels. Unlike earlier transitional stages, the testicular wall was thin; ovarian remnants of any kind were generally absent, and the gonadal tissue was entirely testicular (Fig.1d). All male testes examined had this form.

Dipper and Pullin (1979) found in the temperate labrids *Labrus bergylta* and *L. ossifagus* that sex change occurred only after the reproductive season. In field collections of *C. nicholsi* made over successive summers and winters, ripe females were not found before March, or after mid-July, indicating that the reproductive season is approximately five months long. The occurrence of sex change during spawning months in one all-female pool and in the field suggest that if there is a tendency to change sex in the winter months, the ability to do so is not restricted to any particular season.

Using minnow traps, I caught a total of 804 gobies over a three-year period. The proportional distribution of sexes in different size classes is in accordance with what would be expected in a protogynous hermaphroditic species. There is a marked reduction in the number of females found between 70 and 90 mm SL, concomitant with an increase in numbers of males of that size range (Fig.2). This cannot be ascribed to sex-related size differences since males are on average only a few mm larger than females for any age class (Wiley, 1973). If the decline reflects high female mortality, it does not explain the corresponding increase in numbers of similar-sized males.

I collected 295 females between 30 and 90 mm SL during three reproductive seasons; the smallest individual examined that was carrying ripening eggs, was 50 mm SL. The smallest male examined (31 mm SL) had well-formed crypts of spermatogonia in his testis, in addition to a few oocytes scattered throughout the tissue. If the testis of this male had ovarian origins (the existence of oocytes in a testis is in itself not conclusive evidence for it being a secondary testis; Peters 1975) prematurational sex change occurs in this species.

Males that have developed from females are termed secondary, as opposed to primary males which start life as males. No information is available on sex ratios of newly-hatched or newly-settled larvae in *C. nicholsi*. Therefore, it is not known if all males are secondary, or if some are initially male. Because secondary testes in this species do not have permanent structures indicating former ovarian history, means of distinguishing between secondarily-developed testes and a primary testis (if primary males exist in the population) have not been found.

The reproductive behaviour of *C. nicholsi* is typical of most gobiids (Breder and Rosen, 1966; also see Paper 4). Spawnings I have observed in the laboratory indicate that dominant (i.e., large) males of *C. nicholsi* have the greatest reproductive success within their sex, in terms of acquiring eggs. Because large males are polygynous they probably have a greater reproductive success than adult females of the same age. The size-advantage hypothesis for the evolution of sequential hermaphroditism (Ghiselin, 1969; Warner, 1975) states that sex change evolves when the reproductive fitness is greater for one sex when small-sized, and for the other sex when larger. This circumstance seems applicable to *C. nicholsi*, particularly if spawning success is high in small females.

Since large males have the greatest spawning success, why are small males so prevalent in the population, particularly if some or all of them are secondarily derived? In laboratory groups, small males are attracted to spawning pairs. The opportunity for sneaking (van den Assem, 1967), whereby sperm are released in the vicinity of a courting pair and some fertilization of eggs by the non-courting male is possible, is high (see Paper 4). Hence, small males may have considerable reproductive success through cuckolding larger males. If there is a high cost of egg production to females, at the expense of growth, there may be strong selection under certain social conditions to change from female to male while still small.

Initiation of sex-change in *C. nicholsi* does not appear to be the result of a single factor. Unlike many species demonstrating socially-induced transformation (*Amphiprion* spp., Fricke and Fricke, 1977; *Paragobiodon* spp., Lassig, 1977; *Anthias squamipinnis*, Shapiro, 1981), *C. nicholsi* lives singly rather than in pairs or social groups (although it interacts extensively with conspecifics). In the laboratory, females change sex in the presence as well as the absence of males. Data from laboratory and natural populations suggest that there is no critical size for sex change, as found in *Anthias squamipinnus* (Shapiro, 1981);

most females of *C. nicholsi* transform between 65 and 80 mm SL. The actual size of transformation for different individuals may be controlled by a variety of factors.

E. Acknowledgments

I thank the staff of the Bamfield Marine Station for their help, R. Seward and R. Mandryk for their advice in histological techniques, R. Koss for photographic advice, N. Stacey and R. Warner for help in tissue interpretations, and R. Dubin, J.C. Holmes, J.O. Murie, J.R. Nursall and two anonymous reviewers for criticisms of the manuscript. I am indebted to J.R. Nursall for his advice and encouragement. This project was supported by NSERC Operating Grant A-2071 to J.R. Nursall.

Figure 1. Structure of male, female, and intersexual gonads of C. nicholsi: a) ovary showing central lumen (L) and absence of testicular tissue; b) early intersexual, showing degeneration of ovarian tissue, compression of the lumen, and small nests of cells forming the first spermatogenic tissue (S); c) late intersexual, showing concentration of spermatogenic tissue around the old ovarian lumen; d) testicular, showing anastomosing lumina, each lined with active spermatic tissue. Scale is 200 microns

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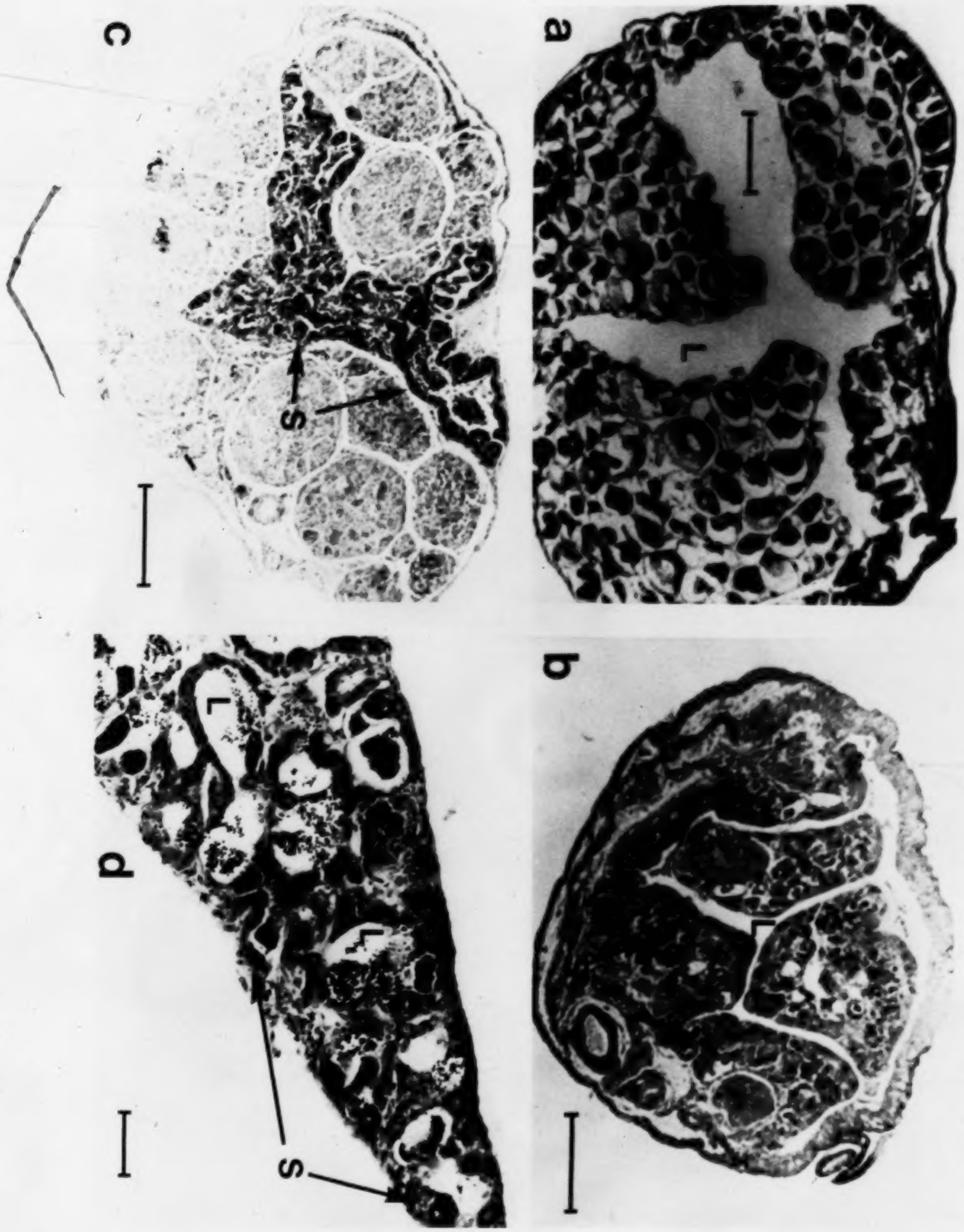
a
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b
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Figure 2. Size frequency distribution of fish collected in minnow traps from 1977 to 1980

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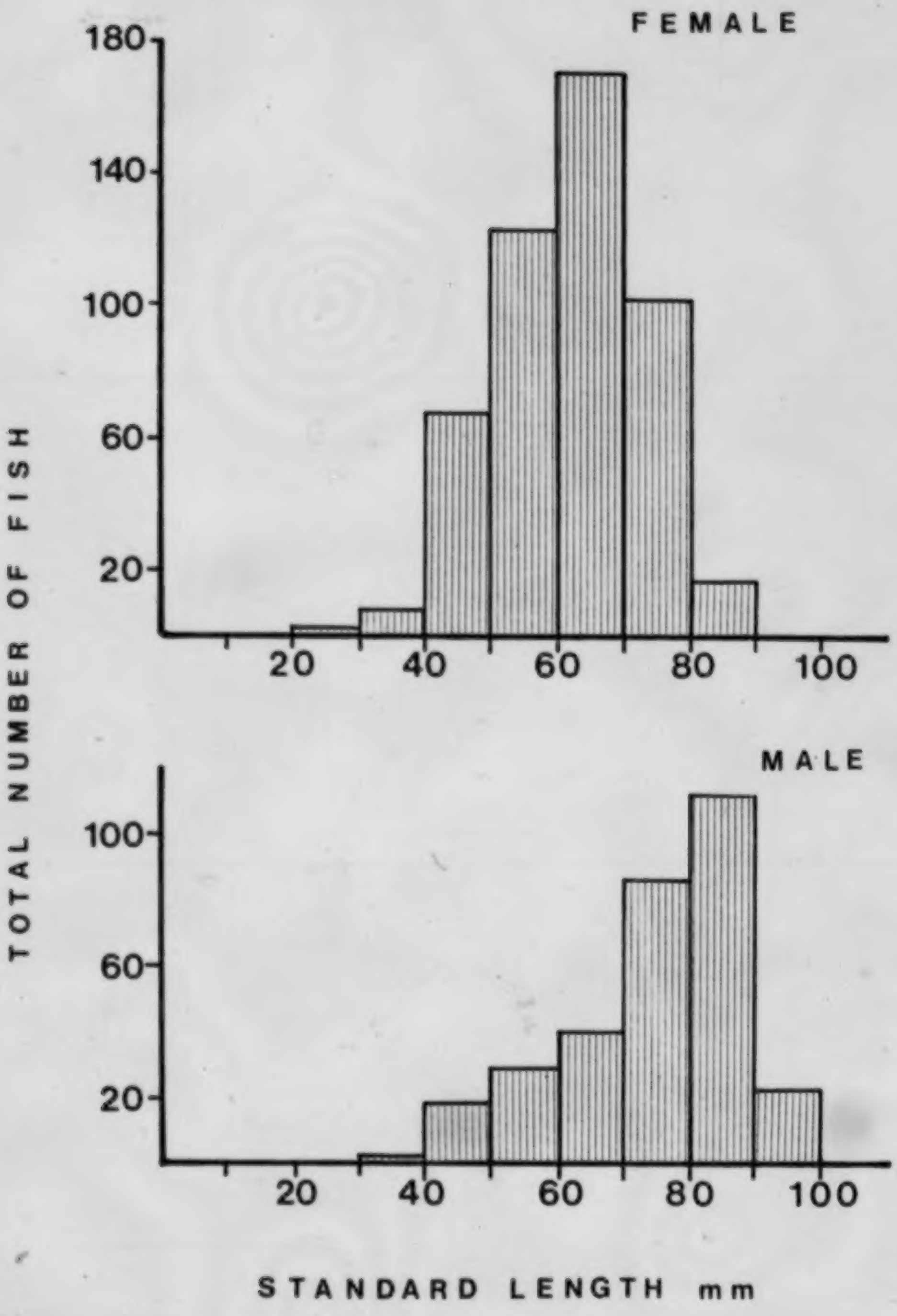
FEMALE
180
140
100
60
20
20
40
60
80
100
MALE
100
60
20
20
40
60
80
100
TOTAL NUMBER OF FISH
STANDARD LENGTH mm

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IV. Paper 4. Male Reproductive Behaviour and Spawning Success in a Temperate Marine Goby, *Coryphopterus nicholsi*

A. Abstract

Coryphopterus nicholsi is a temperate zone marine goby. In laboratory groups of fish, females preferentially spawn with dominant males; assessment of dominance appears to be based upon courting vigour. Male size (standard length) and dominance were often, but not always highly correlated. In contrast, there was no consistent correlation between male territory quality and spawning success. Smaller males in laboratory groups did not court females or guard eggs. However, their behaviour and testicular development during the reproductive season suggest that they may engage in sneak spawning. Dominant males are more likely to successfully guard eggs against conspecific predators than are subordinate males, and hence females should have greater reproductive success if they choose dominant males for spawning partners.

B. Introduction

Coryphopterus nicholsi is a small temperate zone marine goby (maximum 100 mm SL) found along protected rocky shores of the west coast of North America, from the Queen Charlotte Islands to Baja California (Hart 1973). Its preferred habitat, rock rubble interspersed with sand and shell fragments, is widespread but patchily distributed, and the population density within suitable habitat is high, reaching up to eight individuals per square meter in some locations (see Paper 1). Towards the northern end of its range, it is one of the most abundant benthic species in rocky inshore fish communities.

C. nicholsi is territorial (Hart 1973, Wiley 1973, see also Papers 1 and 2). Both males and females of all size classes, including the immature, demonstrate some degree of site constancy and space defence throughout the year. The species is protogynously hermaphroditic, with a predominance of females among smaller fish, and males among larger fish. Overall, there are approximately two females for every male in the population. The reproductive season lasts from early March to mid-July (see Paper 3).

Wiley (1973) supplied a brief description, demonstrating that reproductive behaviour is similar to that of other gobies (Breder and Rosen 1966), but mechanisms for mate choice have not been determined. Because of the importance of mating systems to social organization, I undertook to investigate how male dominance and behaviour influence female choice of a spawning mate, and hence, male reproductive success.

Two main questions were asked: 1) is there a correlation between male dominance or size, or both, and male spawning success in laboratory groups of fish, and 2) what elements of male behaviour influence female choice?

C. Methods and Materials

Fish were collected using minnow traps and sex was determined by external examination of the genital papilla structure (Wiley 1973). Standard length measurements were taken; then individuals were given a small subcutaneous dye mark (Pelikan drafting ink) to aid in individual identification, and placed in separate containers. After a minimum holding period of two weeks, fish were placed into experimental pools. While in isolation, and during the experiments, fish were fed frozen euphausiids twice daily.

Unless otherwise indicated, the pools used were circular, 1.8 m diameter, with water to a depth of 25 cm, and sand shell substrate (a mixture of fine and coarse sand and small shell fragments) to 5 cm. All were supplied with unfiltered fresh sea water (9-11 C) at an approximate rate of 4 l/min. Pairs of overhead fluorescent lights connected to an outdoor photocell provided a laboratory daylength that varied in accordance with natural photoperiod.

All experiments were carried out at the Bamfield Marine Station, on the west coast of Vancouver Island (latitude 49 N., longitude 125 W.), between May 1979 and July 1980.

Observations on groups of fish established during the reproductive season (short-term groups) were initially used to answer the above mentioned questions, but spawning events in such groups may have been influenced by the unfamiliarity of females with males available for spawning. For this reason, supplemental observations were carried out on male spawning success in three groups of fish established at least two months prior to the onset of the reproductive season (long-term groups).

Short-term groups

Three groups of seven males each were established during the reproductive season (Group A, May 1979; Group B, June 1979; Group C, March 1980). In each pool, seven units of cover, formed by one brick propped upon another, were distributed at regular intervals around the periphery, and small stones were scattered about the substrate. In Group A, four bricks were medium-sized (approximately 10 x 10 cm in area) and three bricks were larger (approximately 16 x 10 cm in area). In Groups B and C, all cover was medium-sized. Over the next week, observations on displacement and overt aggression initiated and received by each fish were recorded to determine the dominance rank of each individual. In addition, the locations of displacement and aggressive events, the areas of habitual occupancy, and the areas avoided by adjacent conspecifics were used to determine territory boundaries, which generally were established during the first week.

Bottom maps outlining the pool boundaries and positions of cover and stones were made, and territory boundaries were added. Territory areas were subsequently calculated, using a planimeter.

Approximately one week after the establishment of the experimental groups, a gravid (i.e., distended with eggs) female was introduced into each pool. Upon spawning, the female was removed and another added; females that did not spawn were removed after four days and replaced with another gravid female. Six females were added to each of Groups A and B, and seven were added to Group C. Correlations were then calculated for male spawning success with: male dominance rank (most dominant to least), male size rank (greatest standard length to least), and male territory size rank (largest to smallest). Male spawning success was based on the acquisition of one or more distinct groups of eggs in the nest chamber. The ranking, by size, of male territories was based on the territory size one week prior to the first spawning event in each group. In addition, the ranking was noted just prior to each spawning event within each group over the total reproductive season.

In Group A, after two successful spawnings in the pool, the most dominant (alpha) male was removed, and sequential introduction of gravid females was continued. A second male (the most dominant after the removal of the alpha), was also removed following two successful spawnings. In Group B and C, no male removals were carried out.

In addition to female choice of male, detailed descriptions of male courting behaviour and female responses were made.

Long-term groups

Observations on male spawning success were also carried out on two long-term groups of 14 fish each (seven males and seven females), in which individuals were in groups for five months prior to the reproductive season. These groups were established in September 1979 and maintained until July 1980. Observations were carried out on a third group of 14 fish (also seven males and seven females) established in January 1980, two months prior to the reproductive season, and maintained until July 1980.

In each of these groups, dominance rank and territory areas were assessed as in the short-term experiments. The identity of males successful in obtaining eggs, their standard length, territory size and dominance ranks were recorded, and the dates between which males guarded eggs were noted.

Male behaviour and female choice

To determine the effect of male dominance on male courting behaviour and spawning success, females were presented with two males in which the major difference was one of dominance rank.

Two males of nearly equal standard length (see Table 1) were placed into identical compartments of a subdivided wading pool (Fig. 1), each containing one unit of cover, several small rocks, and two small (≤ 50 mm SL) fish to exercise dominance over. Between the two compartments housing males was a third compartment, also containing cover, into which a gravid female and two additional small fish were placed. All barriers between the compartments were opaque. The fish were left for several days to become familiar with their compartments; all demonstrated dominance over the smaller fish in their compartments within several hours. Following the adjustment period, temporary barriers between compartments were removed, and the gravid female had access to the two males. Because each pool was divided into six compartments, two replicates could be run simultaneously.

Using a 20 channel Esterline Angus event recorder, I recorded the frequency and duration of courting, chasing (aggression directed towards all other conspecifics) and the time spent under cover, over the course of several hour-long observations. Observations continued until the female spawned with one of the males, or released her eggs onto the substrate. After spawning, both males were killed, and their testes removed for histological examination to determine if they contained sperm.

This experiment was repeated with new males and females seven times.

D. Results

Courting and Spawning Behaviour

Courting was observed frequentlyin the laboratory groups of fish. The following description is based on 14 successful spawning events, for which general descriptions of the courting behaviours of males and responses of females were recorded.

Courting by a male consisted of two phases: advertisement and enticement; this was followed by spawning. In the advertisement phase, courting was initiated when the male drifted directly upward from the substrate, and with little fin movement, maintained a stationary position in a horizontal plane 10 to 20 cm up in the water column (hovering). Dorsal, anal, caudal and pelvic fins were all fully extended. Body colour, normally light to orange-tan, with dusky pelvic fins, became pale. The deeply flushed, black pelvic fins and iridescent blue spots under the eyes and on the body stood out in sharp contrast to body colour. Hovering was usually followed by slow, exaggerated, undulating swimming movements, in bouts ranging from 3 to 20 seconds in duration. Then abruptly, the male turned and rapidly swam to the nest entrance in his territory, circled the brick structure, then entered the excavation underneath it. Shortly thereafter, he emerged, swam to some promontory in his territory, perched there briefly, then repeated the process. These events were often interspersed by the removal of sand shell from underneath the cover by the male, and conspicuous deposition of mouthfuls of substrate 20 to 30 cm from the excavation. Sometimes a small piece of shell was picked up, carried for a short distance within the territory, then spat out. All of these behaviours were conspicuous, and attracted the attention of nearby conspecifics. The advertisement phase occurred in the presence or absence of females in the laboratory groups. Uninterrupted bouts of courting behaviour during this phase lasted for over 30 minutes on several occasions.

The enticement phase commenced when a courting male perceived a gravid female. Recognition of introduced gravid females was always rapid, and may be based on the distended abdomen and the brightly tinged pink anal region produced by the presence of egg-laden ovaries. Hovering and exaggerated swimming were directed towards the female. As the female approached the male's territory, courting behaviour increased. Upon approaching the female, the male either rested on the substrate near her for a moment, or swam past her, then pivoted, and rapidly swam to his cover. After going under cover and immediately emerging, he repeated hovering and exaggerated swimming between the female and his cover. Often, the female remained motionless on the substrate near or in the male's territory, with dark mottled colouring and depressed fins. In this case, the male continued to court. If, however, the female showed avoidance behaviour, the male often attacked. If a female approached a courting male's cover, the male often nudged her, in the anal or tail region, towards cover. Sometimes, the male grasped the pectoral fin in his mouth and tried to pull the female under cover. The enticement phase ended when the female entered a courting male's cover, and started to spawn.

Spawning consisted of a female rotating upside down in the excavation and, while moving forward, depositing eggs on the roof of the excavation. Shortly thereafter, the male followed, fertilizing the eggs. Periodically, he would emerge from cover to hover or chase away intruders before rejoining the female. After spawning, up to an estimated 5500 eggs covered an irregular circular patch on the spawning surface. The length of spawning time was difficult to estimate in most cases, because females sometimes emerged between periods of ovipositing, and sometimes stayed under cover after completing spawning. Usually the female was under cover for 10 to 30 minutes.

Other male conspecifics around a spawning pair showed interest in courtship and spawning events. Adjacent territorial males sometimes approached to within 4 cm of the spawning site, well within the boundaries of the resident male's territory. These intruders were often small (50-65 mm SL) territorial males, who were never seen to court females or obtain eggs in laboratory populations.

On one occasion, when a spawning male chased an intruder out of his territory, a nearby small male rapidly went into the excavation with the female and stayed there for approximately 15 seconds until the returning male chased him out.

Histological examination of the testes of seven small males between 48 and 70 mm SL, collected in June 1981, showed that all possessed functional testes with sperm. The testes of these small males occupied a greater proportion of the abdominal cavity than did those of large males collected at the same time, and were usually larger in absolute size than those of large males. Mean weight of pairs of testes removed from seven small males (mean SL=58.3 ± 8.2; range=48.8 to 68.4 mm) was 67.1 ± 27.3 mg, compared to 22.6 ± 3.7 mg for nine large males (mean SL=75.7 ± 3.7; range=70.0 to 80.6 mm).

In long-term groups, the behaviour of males within a group varied in the presence of a gravid female. Behavioural elements that predominated in a dominant male's courting repertoire included hover, go under cover, exaggerated swim, excavating, and perching on promontories (here, cover). In contrast, a fish less dominant than the courting male spent most of its active time chasing conspecifics or moving from cover to cover (traversing) within its own territory. One day after spawning with the female, courting behaviour by the successful male was often still elevated while other fish remained unengaged in reproductive behaviour.

Courting behaviour by smaller or more subordinate males was rarely seen. These fish often remained motionless on the substrate, and occasionally chased intruding fish of both sexes. However, a subordinate's behaviour rapidly changed if, by circumstance, it became the most dominant male among fish not involved in egg-tending. Courting by such males was sometimes observed to be as vigorous as that by the top dominants in the group before they had acquired eggs. Thus male behaviour toward gravid females varied according to it's relative dominance rank among male conspecifics available for spawning.

In seven trials of the female choice experiment, four pairs of males were successfully established each with a single gravid female that subsequently spawned. When the temporary barriers were removed, the two males rapidly established a dominant-subordinate relationship (Table 1) but retained territories with boundaries defined by the earlier position of the barriers; thus the female had a choice of two males of similar size, having equal territory size and amount of cover, but differing in relative dominance rank.

Males successful in obtaining eggs courted more than the unsuccessful male prior to spawning (Fig. 2).

In three of the four trials, the dominant male of the pair courted more than the other male. In Trial 3, carried out in mid-July, however, the alpha male did no courting, and the beta male spawned with the female. A histological examination of the testes of both males (7 micron sections; stained with haematoxylin and eosin) showed no apparent difference in the quality of spermatic tissue, either in terms of abundance of sperm present within the lumina, or in terms of stages of development of spermatogonia. However, the alpha male's testes were approximately half the size of beta's, by volume.

In Trial 4, both males spawned with a small accompanying fish prior to the introduction of a gravid female, demonstrating that both males were fertile, although only one ultimately spawned with the test female.

Over the course of several trials, successful spawning occurred under both units of cover in each choice situation (see numbers, indicating number of spawning events in each compartment, in Fig. 1) indicating no consistent preference for one position of the pool, and therefore one of the two territories, over the other.

Male Dominance and Spawning Success

In all three short-term groups, the first female to spawn did so with the most dominant (alpha) male of the group (Fig. 3). In all cases, general observations indicated that other males briefly courted the gravid female, but only the beta male approached alpha in terms of frequency and duration of courting behaviours.

In two of the three groups (A and C) alpha obtained a second set of eggs shortly after the first spawning event. However, in Group B, no further spawnings took place, perhaps because of the lateness of the season. In Group A, removal of dominants resulted in the acquisition of eggs by subordinates. However, in Group C, from which no fish were removed, the beta fish was successful in obtaining eggs after the alpha fish had obtained eggs from two separate spawnings, was involved in egg guarding, and no longer courted. A female spawned with gamma, whose observed courting behaviour prior to this had been minimal, when both alpha and beta were defending eggs and no longer courting.

Therefore, females consistently spawned with the most dominant courting male in the group. Only the most dominant male obtained more than one set of eggs at a time.

In two of the three short-term experimental groups, dominance rank and size rank were strongly correlated (Table 2a). In general, large individuals were dominant over small individuals. Standard lengths (mm) of males in Group A, in descending order of dominance, were 92.6, 91.1, 71.5, 67.3, 70.4, 67.4, 67.5 , and in Group B, 87.1, 89.2, 80.5, 77.7, 68.3, 67.6 . However, in Group C, the smallest male was the most dominant of six males (measuring 79.5, 85.2, 83.7, 82.6, 84.0, and 81.1 mm SL), and obtained three of the five sets of eggs spawned in that group. Therefore, size was not always an accurate predictor of dominance rank.

In the three long-term groups of fish, over a period lasting from 1 March to 15 July 1980, 24 spawnings occurred, of which 18 were successfully hatched. Abandonment and subsequent egg predation was the cause of egg mortality in the remaining six spawns.

The acquisition of eggs by males within each of the groups was generally dominance-ordered (Fig. 4). Fish of lower dominance usually obtained eggs only after most or all of the higher-ranking males were engaged in egg-guarding behaviour..

In Group 2, the order of acquiring eggs was directly correlated with dominance rank (as calculated prior to the start of the reproductive season) among courting males.

In Group 1, beta obtained its second spawning of the season during a period when alpha had no eggs. However, alpha was in the process of losing its dominance status, and soon after hatching its second set of eggs, died. Shortly thereafter, gamma-a died and gamma-b, after hatching its eggs, lost its dominance status for no clear reason (a and b designations within a rank group indicate close or co-dominance, with neither individual a clear dominant over the other). Therefore, the only fish more dominant than "delta" was "beta", who was already engaged in egg-guarding, and when the next female became gravid, delta was able to court successfully. Thus, mortality in top dominants and reversals in the dominance ranks of some of the remaining fish altered the relationship between spawning success and original dominance rank, but was in accordance with revised dominance ranks.

In Group 3, beta-b obtained eggs after, rather than before gamma-a. However, beta-b's territory was directly adjacent to that of alpha, and shortly after obtaining eggs, was driven out of its territory by alpha, whose own spawn had hatched 24 hours previously. The abandoned spawn disappeared within a week, and because of alpha's frequent visits to the spawn site, predation was suspected as the cause of egg mortality.

On one occasion (Group 2) a female spawned with an alpha male who already had eggs. Both groups of eggs were attached to the same cover surface, and both hatched within a few days of one another with little apparent mortality.

As with short-term groups, dominance rank in long-term groups was correlated with size rank in two of the three groups (Table 2b). Thus, while females consistently chose the most dominant courting male in the experimental group, this was not always the largest male.

Territory Quality and Dominance Relationships

In the short-term experimental groups, territory size upon establishment of these groups was highly correlated with dominance rank; this was not the case, however, when spawning actually occurred (Table 2b). Therefore, spawning appeared not to be dependent upon defence of the largest territory.

In Group A, where cover consisted of regular-sized and large-sized bricks, alpha always defended at least one large cover structure, and in four of five spawnings, the large cover was used for oviposition. In Groups B and C, all covers were similar in size. All successful males defended three or four covers, as did some males who had no spawning success. On three occasions, when an alpha territory became vacant through death or removal, the beta fish made no attempt to take over the missing alpha's territory, and subsequent courting and spawning occurred on the successful males original territories.

In one case a dominant was removed before its eggs had hatched; the eggs were rapidly eaten by the most dominant adjacent territory holder (who was not the new dominant in the group), indicating that conspecific egg predation may be a threat to egg survival.

In long-term groups, neither territory size rank prior to the reproductive season, or at time of spawning, was consistently correlated with dominance (Table 2b) and therefore, with spawning success. The number of units of cover defended by the territory holder, which varied directly with territory size, were similarly unrelated to spawning success (Group 1, $r=.28$; Group 2, $r=0$; Group 3, $r=.50$; Spearman's rank correlation coefficient test; for all values, $p>0.05$). The spawning frequencies on large and small cover units were not different than expected, based on the relative availability of each. Of the 11 males that obtained more than one set of eggs, only one used the same cover more than once. The exception occurred when two sets of eggs were oviposited within several days of one another under the same unit of cover, and were tended together by the parental male.

E. Discussion

In studies of both benthic (van den Assem 1967) and pelagic (Warner et al 1975) spawners, female fish have been shown to spawn preferentially with older, larger dominant males that appeared to occupy high quality territories. When age, size, dominance and territory quality are so closely interrelated it is difficult to determine if females are responding to the quality of the territory, the male, or both.

It is generally held that when male parental care is involved, resource abundance on male territories, nest site, or both are important determinants of female choice (Orians 1969) and that when male parental investment after fertilization is small or non-existent, females tend to choose males solely on the basis of male quality (Trivers 1972). In the mottled sculpin, however, the male tends eggs on a territory site, yet females select only on the basis of male quality, provided the male can provide a site for oviposition (Downhower and Brown 1980).

In this study, females consistently spawned with the dominant courting male, regardless of his size, or the location, size, or quality (in terms of the number of units of cover) of territory. Females appeared to base their choice on the dominance rank of males that were prepared to spawn. However, since this study was confined to the laboratory, environmental characteristics of spawning sites were not examined. Hence one cannot rule out the possibility of site selection *in situ* by *C. nicholsi*, in addition to choice based on male quality.

The removal of dominants was not necessary for less dominant males to spawn successfully with females in experimental groups. However, subordinates usually did not spawn until more dominant fish were already occupied with egg-guarding and no longer courting. The order of acquisition of eggs by males in relation to their dominance rank suggests that in natural populations, dominant males spawn earlier than subordinate males, as has been found in the mottled sculpin (Brown 1981). In *C. nicholsi*, where repetitive spawning occurs throughout the five month, reproductive season, the earlier acquisition of eggs will result in more spawns obtained over the total reproductive season (as was the case in laboratory populations) in comparison to subordinate fish, and hence, greater reproductive success.

The general preference of females to spawn with dominant and (usually) larger males, means that small males will have little reproductive success using conventional courting methods. The disproportionately large testes in small males, and the proximity to ovipositing sites which small males attempt to establish during spawning events, suggest that these individuals employ an alternative reproductive strategy, sneak spawning, to increase their own reproductive success, as has been found in some other fish (van den Assem 1967, Keenleyside 1972). As yet, however, there is no direct evidence for this.

On occasion, males in laboratory groups obtained more than one spawn, suggesting that polygyny may occur in natural populations. In their natural habitat, where rock rubble is abundant, territories often encompass a number of rocks providing suitable spawning surfaces. Hence, the resource critical to gaining multiple mates appears economically defendable, creating an environmental potential for polygamy. Furthermore, sexual receptivity of females in the population appears asynchronous, and females outnumber males; both these factors are also likely to encourage polygyny (Emlen and Oring 1977). If males at the northern end of the range are normally polygynous, it is unclear why more multiple spawning by dominant males was not recorded in the laboratory groups. That may have been due to the ratio of females to males varying from 1:1.5 to 1:2 (due to sex reversals) in the long-term laboratory groups. This was much lower than that normally found (2:1) in field populations (see Paper 3).

Eggs from several females tended to be acquired by a single male within several days of one another. In laboratory groups, males were never seen to obtain more eggs after the first week of tending a spawn, although based on the occurrence of other spawning events in the same group, there was ample opportunity. It may be that males will solicit successive spawns by courting females only for a short period of time following the first spawn, then restrict themselves to tending and guarding eggs until all hatch, before resuming courting. Stickleback males cease courting and become highly aggressive towards females one or two days after obtaining eggs (van Iersel 1953).

In the third experiment, females showed a clear preference for males showing the most courting behaviour. The high correlation between courting behaviour and dominance, together with the correlation of dominance with female choice, suggests that females may use courting vigour to assess male dominance. In *Poecilia reticulata* there is a preference for males with higher rates of display, and females make their choice on the basis of relative rather than absolute rates of courtship (Farr 1980). In my experiments, few competitive courting situations were observed where frequencies and durations of courting behaviour were recorded, but the data suggest that *C. nicholsi* males were also assessed on relative rates of display.

In long-term groups, subordinates courted less in the presence of courting dominants than when the same dominants were guarding eggs and were not courting. Thus, dominant individuals may influence subordinates by suppressing their courtship behaviour. Subordinates can try to "cheat" by courting, but may sustain greater aggression from dominants, as was true for gamma-b in Group 3 of the long-term experiment. In that case, the acquisition of eggs near a more dominant fish with no eggs of its own, resulted not only in the loss of eggs by the subordinate, but also of territory. Such an event, if frequent in natural populations, might alter dominance rank-reproductive success relationships, according to the proximity of a dominant with no eggs, who may interfere with either the courting or egg-guarding process of an adjacent subordinate.

I have no explanation for why the alpha male in one trial of the male courting-female choice experiment did not court, or prevent beta from courting. The small relative size of its testes compared to those of beta, however, and the late date of the trial (mid-July) may indicate seasonal gonadal degeneration on the part of alpha, and a loss of motivation either to court, or to interfere with conspecific courting.

Egg predation has been well documented in the fish literature (van den Assem 1967, Keenleyside 1972, DeMartini 1976, Rohwer 1978). In mottled sculpins, conspecific cannibalism is the primary source of egg mortality (L. Brown, pers. comm.). If egg predation is a common source of egg mortality in *C. nicholsi*, females spawning with dominant males will be choosing a mate that will be a successful egg-guarder on the basis of the ability to repel invading conspecifics. Discrimination of dominant males will therefore be strongly selected for. Females that base their choice on courting vigour in this system will be making a moderately accurate assessment of the relative dominance, and presumably the parenting motivation of available males, at relatively little cost to themselves.

F. Acknowledgments

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Table 1. Standard length (mm) of males placed in pairs with a gravid female. The number in brackets following standard length shows the dominance rank of the individual (1 is dominant, 2 is subordinate). Asterisks indicate fish successful in spawning with the female

Trial 1	Trial 2	Trial 3	Trial 4
85.0 (1) *	85.5 (1) *	82.2 (1)	80.5 (1) *
83.5 (2)	86.7 (2)	82.4 (2) *	78.9 (2)

Table 2. Correlation between dominance rank, size rank (SR) territory size rank before reproductive season (T_1), and territory size rank at time of spawning (T_2), for males in short-term and long-term groups. Numbers in brackets under group headings indicate the number of males in each group; numbers in brackets under T_2 indicate number of males that obtained eggs. The value in each column is r_s, the correlation coefficient (Spearmen's rank correlation); * indicates significance at the 5% level

a) Short-term groups

	SR	T_1	T_2	
Group A (7)	0.74*	0.75*	0.39	(3)
Group B (6)	0.94*	0.93*		(1)
Group C (6)	0.04	0.93*	0.85	(3)

b) Long-term groups

	SR	T_1	T_2	
Group 1 (8)	0.81*	0.57	0.95*	(5)
Group 2 (5)	0.98*	0.93*	0.78	(4)
Group 3 (6)	0.09	0.76	0.80	(5)

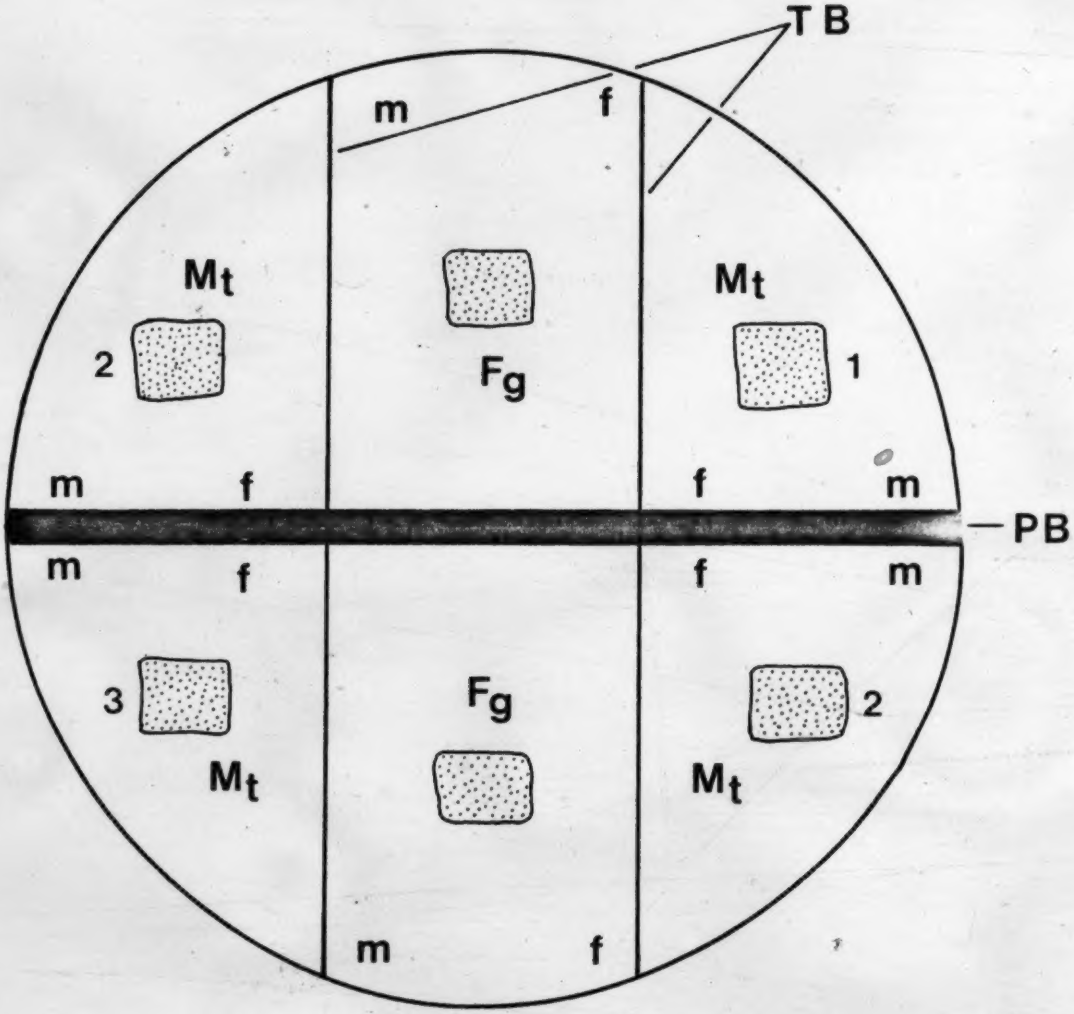

Figure 1. Illustration of the pool used in the male courting-female choice experiment. PB is permanent barrier; TB is temporary barrier. Mt is adult, territorial male; Fg is gravid female; m and f are small (less than 50 mm SL) fish. Numerals indicate number of separate spawning events associated with each unit of cover

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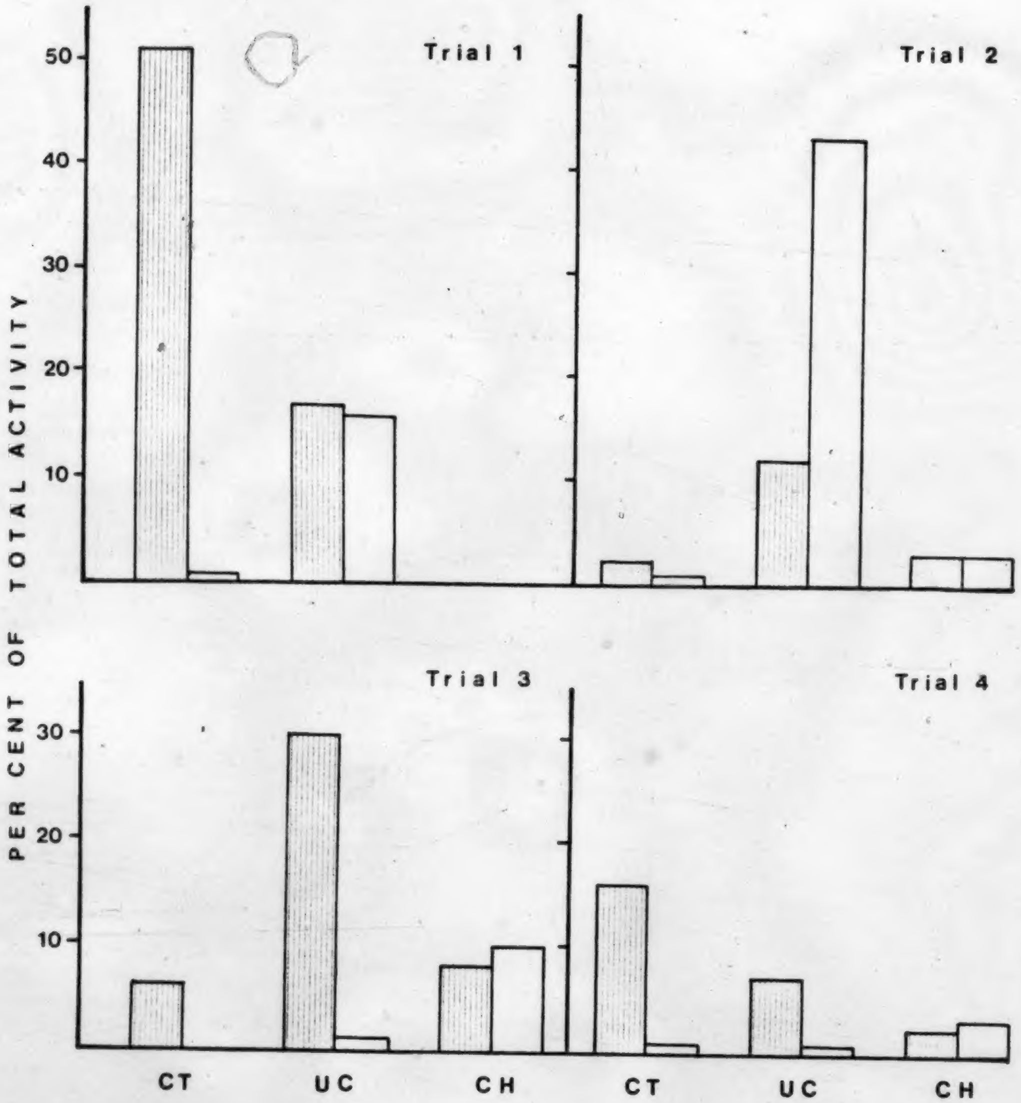

Figure 2. Per cent of total activity devoted to courting behaviour (CT), chasing conspecifics (CH) and sitting under cover (UC), by two males in male courting-female choice experiments. Lined bars indicate males successful in obtaining eggs; open bars represent unsuccessful males.

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Figure 3. Duration of egg-guarding for spawning events in three short-term laboratory groups of fish (Groups A to C). Bars indicate time from spawning to hatching or abandonment (ab); open bars are initial spawns, and cross-hatched bars concurrent second spawns. Dominance rank of males is indicated on the vertical axis.

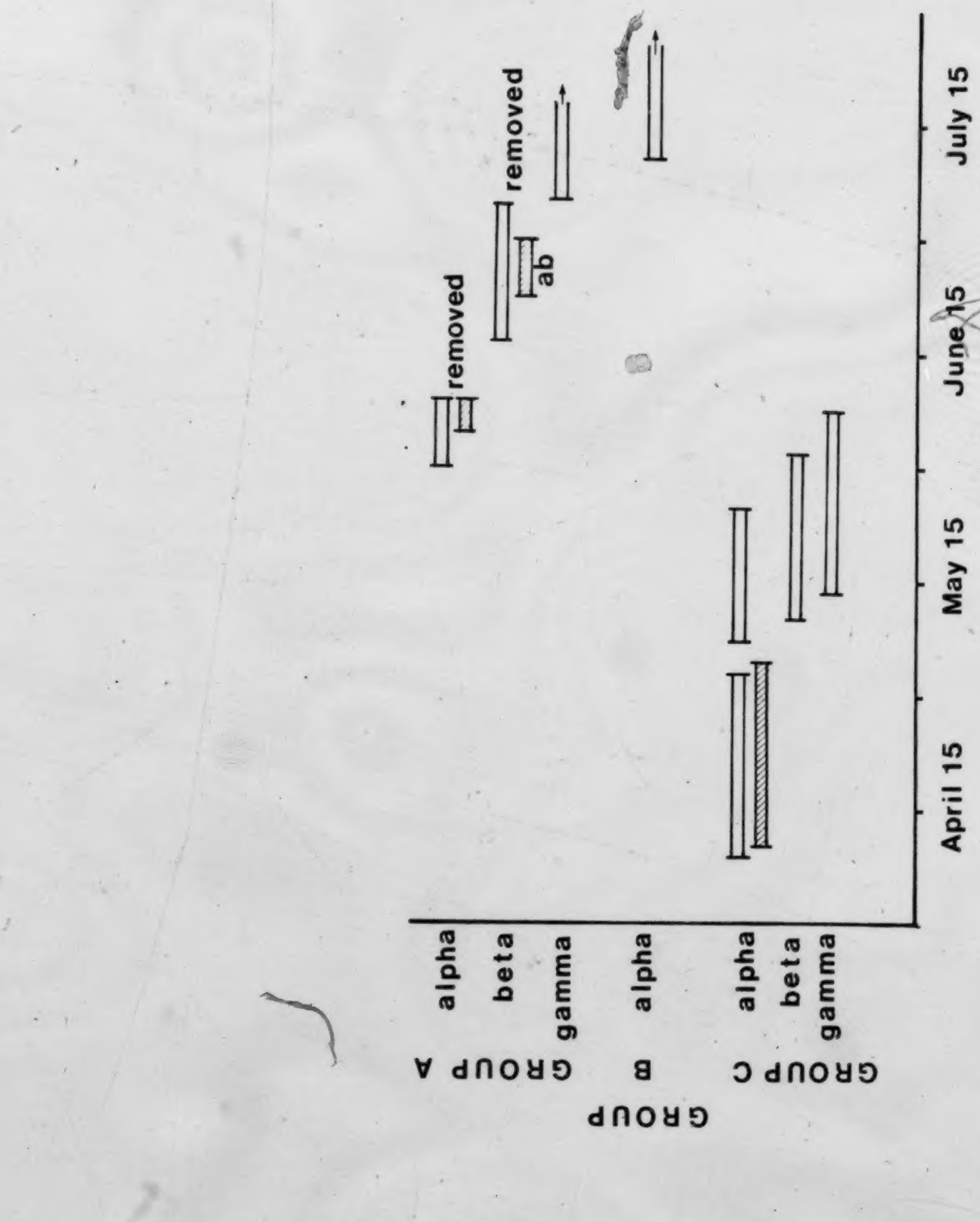
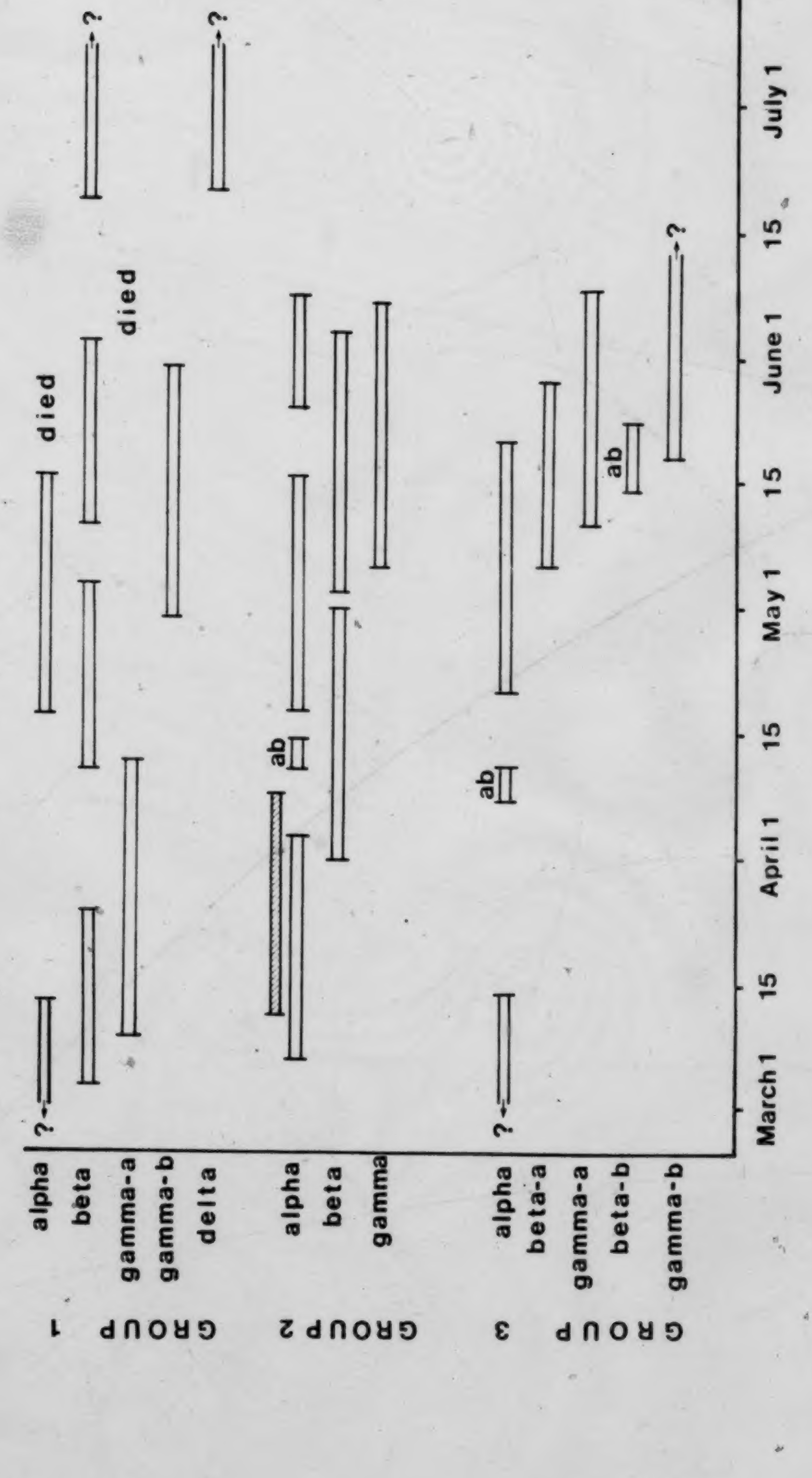

GROUP
GROUP A
alpha
beta
gamma
B
alpha
GROUP C
alpha
beta
gamma
removed
removed
ab
April 15
May 15
June 15
July 15

Figure 4. Duration of egg-guarding for spawning events in three long-term groups of fish (Groups 1 to 3). Bars indicate date of spawning to date of hatching or abandonment of eggs (ab), of individual males, whose dominance rank is indicated on the vertical axis. Letters following some dominance ranks (a and b) indicate individuals of approximately equal dominance rank. ? indicates that date of spawning or hatching is unknown. Cross-hatched bars indicate the presence of a second spawn when a first is already being tended.


GROUP 1
alpha
beta
gamma-a
gamma-b
delta
GROUP 2
alpha
beta
gamma
GROUP 3
alpha
beta-a
gamma-a
beta-b
gamma-b
died
died
ab
ab
ab
?
March 1
15
April 1
15
May 1
15
June 1
15
July 1
15

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V. Paper 5. Resource Defense in a Territorial Temperate Zone Pacific Goby,*Coryphopterus nicholsi*

A. Abstract

Coryphopterus nicholsi is a territorial, temperate zone goby that occupies rock rubble and sand substrate in protected subtidal waters. Defence of territories is exhibited by all members of the population throughout the year. Reproduction, feeding, and the use of cover to avoid predators and strong water currents are all potential functions of space defence. Reproduction is seasonal; females spawn in male territories and males alone guard the eggs until hatching. The territories of females and small non-courting males appear to serve no direct reproductive function. Territories show peripheral overlap between conspecifics, particularly between fish of different size classes. Feeding is both benthic and planktonic. Fish of different size classes may partition food resources on the basis of prey size and prey type, but stomach content data are inconclusive. The use of shelter providing cover appears common to all individuals. In the field, refuge is provided by excavations under rock. Territory overlap in field and laboratory populations rarely included areas with refuge. In laboratory experiments, structures providing cover determined the location of territory. In field populations,

cover provides nocturnal refuge, protection from displacement by water action, and protection from predators. Cover appears to be the primary resource determining territorial organization in this species.

B. Introduction

Coryphopterus nicholsi, the blackeye goby, is a common inhabitant of subtidal rock rubble along much of the western coast of North America. Its known range extends from Baja California to the Queen Charlotte Islands of British Columbia (Böhlke and Robins 1960, Hart 1973). It has been described as territorial (Ebert and Turner 1962, Wiley 1973, also see Papers 1 and 2), but reasons for space defence have not been reported.

Reproductive behaviour in *C. nicholsi* is typical of many gobies (Breder and Rosen 1966). The breeding season lasts for five to seven months (Wiley 1973, also see Paper 3). Parental care in the blackeye goby is restricted to the males and consists of guarding and tending the eggs; after hatching, the larvae enter a planktonic stage for an undetermined period of time prior to settling (Wiley 1973). Field observations and laboratory experiments show that the ability to defend space is universal in this species, being evident in fish of both sexes, of all sizes (post-settlement), at all times of the year (see Paper 1). Because of the uniparental and seasonal nature of reproduction, universal space defence would not be predicted on the basis of nest site defence alone. Hence, some other resource(s) must be of importance in the establishment of territoriality.

Two resources commonly associated with territorial behaviour, in addition to defence of a site for reproduction, are food and refuge. *C. nicholsi* is a generalized predatory species, its members feeding on both benthic and planktonic organisms (Wiley 1973). I found that large fish defended larger territories than smaller fish (see Papers 1 and 2), in both field and laboratory populations, suggesting the possibility that defended space protects a food resource. However, territories were not completely exclusive; peripheral overlap with other territories was common, particularly among fish of different size classes. The use of territories primarily for feeding would only be predicted if fish of different size classes have a low dietary overlap, and hence do not compete for the same food resource. To determine if food habits of different-sized fish could be clearly separated on the basis of size or type of prey, an analysis of stomach contents was carried out on two groups of fish, one collected during the winter and another during the summer.

Refuge is also an important resource for many territorial fish (Moran and Sale 1977, Phillips 1977, Phillips and Swears 1979). *C. nicholsi* defended and used structures offering cover or visual isolation in both laboratory and field populations (see Papers 1 and 2). It is not known whether such structures primarily offered protection from water movements that might displace individuals, from predators, or both. However, if such refuge is important in space defence, its location should influence territory location. Therefore, a set of laboratory experiments was designed to determine the role of structures offering cover and visual isolation in site preference of territorial fish. In addition, to determine the role of cover in predator avoidance, I recorded the use of cover by *C. nicholsi* during interactions with other common inhabitants of its habitat.

C. Methods and Materials

Experiments were conducted at, and fish collected in the vicinity of, Bamfield Marine Station, Barkley Sound, Vancouver Island. To examine stomach contents, two collections of fish were made, one in January and one in June 1981, using 2-phenoxy-ethanol fish anaesthetic. Fish were killed within two hours of capture. The stomach and gut contents were removed, placed in 5% buffered formalin, then transferred to 30% isopropyl alcohol. Prey items were subsequently identified and measured along the longest axis. The type and total number of prey items were then compared between fish of different size classes.

Underwater observations with SCUBA were made on four $4m^2$ study quadrats, located at the mouth of Bamfield Inlet (see Paper 1 for a detailed description), to determine the role of cover in predator avoidance. Fish within each quadrat were watched during periods of approximately 40 min; all observations totalled 54 hours. Interactions were recorded between *C. nicholsi* and other heterospecifics commonly found in the same habitat, and avoidance responses of *C. nicholsi* were noted.

Lastly, to examine the role of cover in laboratory populations, fish were collected in unbaited minnow traps throughout the year. Their sex was determined by examination of the genital papilla (Wiley 1973, see also Paper 2). They were measured (standard length), dye-marked with subcutaneous injections (Pelikan drafting ink,) and held in isolation in individual holding containers prior to experimentation. All experiments were performed in circular wading pools measuring 1.8 x 0.3 m, supplied with fresh sea water at a rate of 4 l per minute. A 2 cm layer of sand and shell fragments covered the bottom of each pool, and scattered small stones acted as visual landmarks. Three experiments were carried out. Experiment 1 ran from 2 September to 5 October 1978; water temperatures were from 13-15 C and daylength was 14 hours. Experiment 2 ran from 20 October to 10 November 1978 and Experiment 3 ran from 1 October to 28 November 1979. In the second and third experiments, water temperatures were 11-12 C and daylength was eight hours.

In Exp.1, 10 fish (five of each sex) were introduced into each of two pools, designated Pool F and Pool G. Fish were matched for size between pools (Table 1). During a two-hour period following introduction, the identity of each fish in an interaction and the outcome of the interaction were noted so as to determine the dominance ranks of all fish in each group. This procedure was repeated on the second day and again on the seventh day after introduction. Following this, the territorial boundaries of the fish that defended space were determined by recording peripheral points of defence or unchallenged movement by each fish, as well as the areas or points of avoidance by adjacent fish. When territory boundaries of the three most dominant fish (alpha, beta and gamma) had become established, cover was introduced. In both pools, one unit of cover, consisting of one brick propped upon another, was placed on the pool periphery at a point farthest from the territory of the alpha fish. Following the introduction of bricks, changes in the location of territories of fish were noted. After new territory boundaries had been established, a second unit of cover was added at the opposite side of the pool from the first unit of cover and changes in the territory boundaries were noted. Subsequent manipulation of the two brick structures followed. Manipulation involved converting cover to "visual isolation" by dropping the propped brick to the substrate, as well as interchanging the positions of cover and visual isolation. With visual isolation structure, fish could hide behind or between the two bricks, but not under them.

Following the manipulation of cover and visual isolation in Exp.1, fish were removed and returned to individual holding containers for a period of two weeks. During this time, fish were exposed to reduced daylength and lowered water temperature. In Exp.2, the fish were returned to their respective pools, without cover. After new territories were established and dominance ranks again assessed, structures were introduced into each pool. One unit of cover and one unit of visual isolation were placed at opposite sides of the pool, but both outside alpha's territory. Cover was placed farther from alpha's territory than was the unit of visual isolation. After recording changes in territory locations, the location of cover and visual isolation were interchanged. Lastly, a second unit of cover was introduced to the pool periphery, equidistant from the other two brick structures, and outside the former and present locations of the alpha territory.

In Exp.3, new groups of fish (six males and four females) were established in each of two pools, designated Pool 1 and Pool 2. As with the first two groups, fish were matched as closely as possible for size between pools (Table 1). Exp.3 was carried out in a similar manner as the preceding experiments, with two exceptions. Following the structural manipulations, first the alpha, then the beta fish were removed. Changes in the location of site defence were noted after each removal. In addition, nocturnal checks on the users of cover and visual isolation were made. This involved placing an enclosure around the structure and examining the occupants by flashlight, two hours before lights normally came on. In the case of cover; the leaning brick was temporarily removed to expose any occupants underneath.

Lastly, in 54 hours of underwater observations by SCUBA, avoidance interactions were recorded between *C. nicholsi* and heterospecifics commonly found in the same habitat.

D. Results

Stomach content analysis

Twenty-eight fish were collected in January 1981, and fifty-nine in June 1981. In the latter sample, two had empty stomachs. Fish from each collection were divided into three size groups matching those used in field observations (see Paper 1): small fish, less than 55 mm SL; medium-sized fish, 55-70 mm SL; large fish, greater than 70 mm SL.

In both collections, small fish predominantly ate small (less than 1 mm) prey items (Table 2). These included both planktonic cyprid larvae and benthic organisms such as cumaceans, harpacticoid copepods and gammarid amphipods. In general, larger-sized fish ate larger-sized prey items, ostracods being an exception. Large fish also ate more barnacles, bivalves and gastropods than did small-sized fish. Medium-sized fish tended to eat a large number of isopods and gammarid amphipods.

A greater number of fish scales was found in the stomachs of larger fish. Since no skeletal remains of fish were present, the scales were probably a result of aggression-related nipping rather than predation.

Some prey organisms, typical of the winter sample (i.e., gastropods), were absent from the summer sample. Similarly, cyprid larvae, cumaceans and nematodes, which were abundant in the summer sample, were not found in winter stomach contents.

Heterospecific interactions

Six other species in addition to *C. nicholsi* were seen regularly on or moving just over the observation quadrats: kelp greenling (*Hexagrammos decagrammus*), painted greenling (*Oxylebius pictus*), juvenile rockfish (*Sebastes* spp.), ling cod (*Ophiodon elongatus*) and striped sea perch (*Embiotoca lateralis*). Less often seen were ratfish (*Hydrolagus colliei*).

Large kelp greenling (300-400 mm SL) were abundant on the study site. Movements of greenlings through goby territories were frequent, and attacks on gobies were common.

Ling cod, another common fish on the quadrats, evoked no response from nearby gobies unless they moved rapidly by or directly over a goby territory, in which case, gobies moved under cover.

On one occasion, a cormorant (*Phalacrocorax* sp.) appeared on the study site and foraged along the bottom, periodically inserting its bill into crevices. All gobies within my range of sight (approximately 5 m) disappeared under cover and stayed there until the cormorant, after repeated dives, left the area about 10 minutes later.

In marked contrast to these reactions, gobies demonstrated no avoidance response to either striped sea perch or ratfish. The diet of both these fish is restricted to invertebrates.

Response to cover

Table 3 shows the responses of the most dominant (alpha) and second-most dominant (beta) fish to the introduction and movement of structures offering cover. In Exp.1, in both Pool F and G, alpha preferentially occupied and defended cover. Cover was preferred over structures providing only visual isolation, and territories were moved to accompany shifts in the location of structures offering cover. Beta preferred visual isolation over no structure, and when available, cover over visual isolation. However, if only one structure was present, alpha defended it and beta defended an area outside alpha's territory borders.

In Exp.2, responses of the same two groups of fish to the addition and alteration of structures were unchanged (Table 4), although water temperature and photoperiod were decreased.

In both Exp.1 and 2, other fish sometimes used and defended cover and visual isolation. When a principal defending fish was temporarily elsewhere, the most dominant of the adjacent subordinates with no structure of its own immediately occupied and defended the structure. If it left for some reason, the next most dominant fish took over. As a rule, more subordinates demonstrated this form of defence of beta's structure than that of alpha; often, alpha's structure was unused by other fish, even in its absence. In all cases, access to a defended structure was dependent upon the relative dominance rank of contesting individuals.

In Pool G of Exp.1, the response to structures offering total or partial cover was complicated by the creation of excavations by some fish. These excavations were formed by the removal of gravel immediately adjacent to one or more landmark rocks. By occupying the depression thus created, often against the side of a rock having a slight overhang, a fish could experience some of the features offered by the visual isolation structure. Typically, it was the beta fish that defended such an excavation. Only once was the alpha fish in Pool F or G observed to exhibit this type of defence.

The attractiveness of such excavations became more evident in Exp.3 (Table 5). In both pools, excavations were used extensively, and were shared much in the same manner as cover and visual isolation-sharing in former experiments. However, the addition of nocturnal checks on cover and visual isolation users may have diminished the desirability of these structures and consequently enhanced the attractiveness of excavations that were less protective, but also less disturbed. The pattern of the alpha fish defending cover, beta defending visual isolation, and subordinates sharing defence of these structures on a dominance rank basis, was maintained during the initial stages of the experiment, prior to nocturnal checks.

The identification of fish occupying cover and visual isolation in the early morning, prior to the onset of light, yielded unexpected results. Several fish were found to share both structures, (Table 6). This is in marked contrast to diurnal behaviour, when structures were occupied by only one fish at a time.

Upon the removal of the alpha fish from each pool, beta immediately adopted cover. In Pool 1, gamma occupied cover upon beta's removal; in Pool 2, gamma retained occupation of the excavation, rather than moving to cover.

E. Discussion

Territories have frequently been described for fishes consuming benthic prey (Low 1971, Vine 1974) and water-borne prey (Keenleyside 1962, Slaney and Northcote 1974). *C. nicholsi* appears to have a highly varied diet of both benthic and planktonic prey items, including many crustaceans and molluscs. Wiley (1973) found that *C. nicholsi* at the southern end of the range also had a high proportion of crustaceans and molluscs in its diet, in addition to annelids, echinoderms and bryozoans. However, he did not find gross differences in diet between size classes.

Any interpretation of the results presented here is limited by the small sample size. However, the results suggest that fish of different size classes may have different preferences in both prey size and prey type. Small fish appear to take smaller prey than large fish, and this may result in preferences for different prey types. Larger fish ate many more hard-shelled organisms than smaller fish. Although such prey items may require greater crushing power or larger teeth, most shells were found intact in the stomach. The lack of such organisms in small fish stomachs may indicate differences in prey choice.

Whether dietary differences are sufficient to reduce food competition among size classes and permit spatial overlap in territories that are used for feeding, is unknown. A more rigorous examination of diet is necessary before the extent of food preferences can be accurately assessed. On the basis of these results, however, a feeding function for territoriality cannot be ruled out.

The greater amount of peripheral overlap between different size classes found in field populations may reflect the importance of factors such as settlement patterns, topographical heterogeneity, and smaller space needs of smaller fish, in addition to possible diet differences. When young fish settle on a suitable substrate, they are able to occupy and defend areas interstitial to territories of large fish, because of their small size. Therefore, they can use areas of suitable habitat too small to support larger fish. In addition, their small size will enable them to remain less visible to adjacent dominants than their larger conspecifics.

The results of the laboratory experiments show that structures offering cover are important in determining the location of territory. The use of cover serves many functions. Cover is used at night for refuge (see Paper 1). In addition, during peak periods of tidal flow, water currents are strong and most fish remain close to the substrate, often partially under cover (pers. obs.). During winter months, when wave action is heavier and water conditions are generally turbulent, it is likely that cover offers similar protection against displacement by water action.

Field observations of the reactions of gobies to predators showed that cover was also used in predator avoidance. In the laboratory, a strong preference for cover over visual isolation was demonstrated. If the main function of defended structures is antipredatory, this would be expected, as structures providing visual isolation offer less protection than cover. Phillips (1977) found that the banded blenny, (*Chasmodes bosquianus*), preferred closed shelters to open shelters, and stated that shelter use was most probably related to avoidance of predation.

In laboratory populations of *C. nicholsi*, access to cover was dominance-dependent, suggesting that cover generates competition. Phillips and Swears (1979) found that dominant banded blennies had priority of access to shelter, and by using protective shelter, escaped attack from predators significantly more often than did subordinates. The high number of piscivorous predators present in the habitat of *C. nicholsi* suggests that predation pressure may be great. The rarity with which territory overlap included areas of cover in field populations (see Paper 1) emphasizes the apparent importance of refuge to territory holders. The importance of cover in these contexts suggests that predation may be a major determinant of territorial behaviour in this species.

Demonstrating territorial defence of a resource depends upon showing that the resource in question is limiting. Cover for this species is created by excavations under rocks, and along northwest Pacific shores, rock is abundant. How can this resource be limiting?

Distribution of *C. nicholsi* is limited to protected shores having rock rubble interspersed with sand and shell-fragment substrate which allows for excavation. Such habitat is patchily distributed and population densities within patches are high, reaching 8 fish per m^2 (see Paper 1). The establishment of new habitat (concrete block reefs) within 10 m of goby habitat resulted in rapid colonization by both large and small gobies (Gascon 1982), suggesting that suitable habitat is limited.

Within rock rubble patches, not all rock is suitable for excavation. Small rocks are liable to shift in winter storm surge, and many large rocks are set too deeply into the substrate to permit excavation under them. Hence, within occupied habitats, appropriate rock may also be limited.

Why then is cover not shared by individual fish, as occurred in laboratory populations? *C. nicholsi* tends to forage away from cover. In emergency retreat circumstances, a convergence of several individuals at a single refuge entrance would reduce escape chances for all. Hence, the value of cover as refuge from predators would be reduced if shared. On a single night dive, an examination of refuge excavations indicated that nocturnal use of refuge was solitary (see Paper 1). The nocturnal sharing of cover found in the laboratory may therefore reflect conditions imposed by the experiment, generating aberrant responses. It may also indicate increased tolerance to conspecifics at night, when fish are already under cover, and rapid escape routes are not needed.

Large males use cover as a spawning site for five months of the year (see Paper 4). Winter defence of cover would guarantee a summer spawning site for these individuals. Smaller males, in contrast, appear to have low courting success, and territories may serve no reproductive function. Females do not spawn in their own territory, since they engage in no parental activity. As tranformed males, they may defend a spawning site at some time in the future, but whether it is the same site, or a new one, is unknown. Therefore, an argument cannot presently be made for the evolution of a territorial social system to guarantee possession of a spawning site for immediate or future use by all members of the population. Access to cover is likely the prime factor promoting territoriality in this species, for without defence of a suitable space providing cover, many individuals are not likely to reach reproductive age.

F. Acknowledgments

I am indebted to the late J. Baron, and to C. Haylock and P. Smith, for help in laboratory maintenance, to M. Prekker for help with fish care, and to R. Miller for assistance in underwater observations. Helpful criticisms of various versions of the manuscript were given by R. Dubin, J.O. Murie, D.L.G. Noakes, J.R. Nursall, T.M. Stock and two anonymous reviewers. I am grateful to J.R. Nursall for his encouragement and financial support during the course of this work. This research was supported by NSERC Operating Grant A2071 to J.R. Nursall.

Table 1. The sex, standard length (mm) and dominance rank, respectively, of all fish within each experimental pool. M is male and F is female. Dominance rank from high to low ranges from 1 to 10. Fish of equal dominance are assigned ranks of equal value

POOL F			POOL G			POOL 1			POOL 2		
M	91.8	2	M	94.9	2	M	95.0	1	M	93.2	1
M	84.4	1	M	85.9	1	M	95.0	2	M	90.1	3
M	84.0	3	M	85.2	3	M	88.4	3	M	84.5	2
F	80.3	4	F	79.1	4	M	84.4	4	M	82.5	9.5
M	79.5	6	M	77.1	5	M	81.5	5	M	80.7	4
F	69.6	8	M	77.1	7	M	81.5	6	M	79.2	5
M	69.4	5	F	69.2	8	F	72.3	8	F	70.1	6
F	67.5	7	F	68.8	6	F	72.3	10	F	70.0	9.5
F	64.6	9.5	F	60.2	9.5	F	72.0	7	F	69.7	7.5
F	55.1	9.5	F	55.2	9.5	F	65.8	9	F	68.4	7.5

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Table 2. Number of prey items found per fish in each size group (<55 mm standard length, 55-70 mm, >70 mm) for winter and summer collections. All prey items measured less than 1 mm along the longest axis, unless otherwise indicated

Prey	Prey Size	Winter			Summer		
		<55	55-70	>70	<55	55-70	>70
Cyprid larvae		0	0	0	29.4	9.3	1.9
Cumaceans		0	0	0	3.2	1.2	0
Nematodes	>2.0	0	0	0	0.2	0.2	0
Ostracods		1.0	2.5	2.3	0.6	0.9	2.0
Isopods	≤1.0	0	0.5	0.1	0.4	0.4	0
	>1.0	0	0.1	0.2	0	0	0
Harpacticoid Copepods		5.6	1.6	0.5	0.2	0.3	0
Foraminifera		0	0.5	0.4	0.4	0.4	0.1
Gammarid Amphipods	<0.5	0	0	0	0.8	1.7	1.1
	0.5-1.0	4.0	1.6	0.2	0.2	0.1	0.7
	1.0-2.0	0.4	0.5	0.7	0	0.1	0
	> 2.0	0.6	0.9	0.6	0	0	0
Scales	Goby	0	0.1	3.0	0.2	1.0	7.4
	Other	0	0	0	0.2	0.5	3.4
Barnacles		0.2	0.2	1.5	0.3	0.4	1.3
Gastropods	<1.0	0	0.2	1.0	0	0	0
	1.0-2.0	0	0.6	1.1	0	0	0
	>2.0	0	1.0	0.6	0	0	0
Bivalves	<0.5	0	0	0	0.4	1.0	1.6
	0.5-1.0	0	0	0.2	0	0	0.1
	>1.0	0.2	0.1	0.2	0	0	0
Decapods	≤2.0	0	0.2	0	0	0	0
	>2.0	0	0.2	0	0	0	0.4
Sample Size		5	13	10	26	24	7

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Table 3. Responses of the alpha and beta fish to introduction and removal of cover and conversion of cover to visual isolation in Experiment 1, for Pool F and Pool G. Entries under alpha and beta columns indicate structures occupied and defended by those fish, respectively. C is cover and VI is visual isolation. Superscript distinguishes cover introduced first from cover introduced second. * is excavation

POOL F

Cover Condition	Alpha	Beta
+ Cover^1	C^1	Other
+ Cover^2	C^1-C^2 C^1	C^2
- Cover^1	C^2	Other
- Cover^1	C^2	Other C^1 Other
Cover^2 → Visual Isolation	C^1	V.I.

POOL G

Cover Condition	Alpha	Beta
+ Cover^1	C^1	Other
+ Cover^2	C^2 C^1 Near C^1-C^2 C^1-C^2 C^1	C^2 C^2 Near C^2 C^2 C^2
Cover^1 → Visual Isolation	C^2	V.I. *
Cover^2 → Visual Isolation	C^1	Other *

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Table 4. Responses of the alpha and beta fish to introduction and interchange of cover and visual isolation, in Experiment 2. Entries under alpha and beta columns indicate structures occupied and defended by those fish, respectively. C is cover and V.I. is visual isolation. Superscript distinguishes cover introduced first from cover introduced second. * is excavation

	POOL F		POOL G	
Cover Condition	Alpha	Beta	Alpha	Beta
+ Cover^1 & Visual Isolation	C^1	V.I.	C^1	V.I.
Cover$^1 \leftrightarrow$ V.I.	C^1-V.I. C^1	Other	C^1 C^1-V.I.-* C^1	V.I. Other*
+ Cover^2	C^1-C^2 C^2	Other Other	C^1-C^2-V.I. C^1	Other* V.I.-C^2

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Table 5. Responses of alpha and beta fish of Pool 1 and Pool 2, to cover, conversion of cover to visual isolation, and to disturbance of nocturnal checks, in Experiment 3. Responses of gamma fish are added with removal of alpha and beta fish. Alpha, beta and gamma columns indicate structures occupied and defended by those fish, respectively. C is cover and V.I. is visual isolation. Superscript distinguishes cover introduced first from cover introduced second. * is excavation

	POOL 1		POOL 2	
Cover Condition	Alpha	Beta	Alpha	Beta
+ Cover^1	C^1	Other	C^1	Other
+ Cover^2	C^1 C^2	C^2 C^1	C^1-C^2 C^1	C^2 C^2
Alpha Cover → V.I.	C^1	Other*	C^2-V.I.	V.I.-*
After Nocturnal Checks	C^1-V.I. C^1-*-V.I.	V.I.-* C^1-*-V.I.	* V.I.* C^2-*	C^2-* C^2-*-V.I. C^2-*
Cover ↔ V.I.	C^2	V.I.-*	C^1	V.I.
	Beta	Gamma	Beta	Gamma
- Alpha	C^2-* C^2-*	Other V.I.-*	C^1 C^1-*-V.I.	* *
-Beta		C^2-*		*

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Table 6. Number of fish found using cover and visual isolation (V.I.) prior to onset of light, in Experiment 3

	POOL 1		POOL 2	
Date	Cover	V.I.	Cover	V.I.
Nov. 7	None	2	4	2
Nov. 13	2	2	3	4
Nov. 14	None	1		
Nov. 16	2	None	3	None
Nov. 19	1	3	2	3
Nov. 20	4	2	3	2
Nov. 21	1	2	2	None

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Concluding Discussion

The purpose of this study was to examine the relationship between social behaviour and patterns of space use in the temperate zone marine fish *Coryphopterus nicholsi*, and subsequently to determine what resources may be important for a territorial social system in this species.

Field and laboratory studies show that *C. nicholsi* deonstrates a high degree of site attachment and site defence, and that territorial behaviour was demonstrated within the same habitat by all members of the population, throughout the year. However, fish generally defended areas only against same-size or smaller fish.

The pattern produced by territorial partitioning was neither spatially regular nor consistent over time. The size of territory varied directly with the size of the holder. Typically, territories had a central area that was used exclusively by the territory holder and contained cover Towards the periphery of defended areas, spatial overlap occurred with other territories. This overlap was often between fish of different size classes. However, the use of areas of overlap was not equal between conspecifics. Generally, the larger of the two fish had unchallenged access to the overlapped area; the smaller fish defended this area only in the absence of the larger fish.

Territories defended by small fish often had exclusive areas that were interstitial to the adjacent territories of larger fish. By frequently moving from an area of overlap within one territory, to another, and by using interstitial refugia, smaller fish were able to coexist with larger fish.

The resulting pattern of smaller fish occupying interstitial areas, with more territorial overlap between size classes than within size classes, produced a complex distribution of territories. Fish within the same general size class formed a single territorial mosaic. Territories of all size classes togeather produced a superimposition of several mosaics.

Simple mosaics have frequently been described in fish (Keenleyside 1979). Populations showing a non-overlapping formation are usually monomorphic, as with same-size juvenile salmonids (Slaney and Northcote 1974) that hold feeding territories, and adult cichlids (Barlow 1974) defending reproductive territories. However, more complicated patterns of space use have been described in other fishes (Keenleyside 1972, Nursall 1977, Larson 1980), and two common factors appear to be involved; territories are permanent rather than short-term, and the habitat is occupied by adult males and females, as well as immature fish.

Field observations did not indicate seasonal changes in territory size. However, in laboratory populations, territories of some individual fish followed through a non-reproductive and subsequent reproductive season showed considerable changes in territory size. Many territories of dominant, spawning males increased during the period of reproduction. The territories of other fish did not significantly decrease. This infers that more of the substrate was utilized during the reproductive season.

Population density was high in field populations, and unused habitat was likely unavailable. If territory expansion during the reproductive season occurred in the field, some individuals in the population, such as small interstitial fish, should be displaced from their territories. Alternatively, adjacent subordinates could reduce their territory size to accommodate the increased space demands of larger male neighbours.

Space defence in laboratory populations was also affected by the parental state of males during the reproductive season. The size of the exclusive portion of a male's territory increased significantly when a male was guarding eggs. The most likely reason for the lowered tolerance of conspecifics at this time was to reduce the occurrence of conspecific egg predation.

The preceding findings show that the spatial distribution of territories in *C. nicholsi* is variable between individuals and over time. However, there is another factor influential in the partitioning of space by this species. Space defence was usually exercised against same-size or smaller conspecifics in both field and laboratory populations, suggesting that there is a dominance hierarchy operating within the social organization of *C. nicholsi*.

Laboratory populations demonstrated the importance of dominance rank with regard to the successful defence of space. As with many fish, size rank and dominance rank were highly correlated. Dominant fish had priority of access to space; in areas of overlap, subordinates could only use and defend space in the absence of dominant individuals. Thus, the pattern of overlapping mosaics is actually a spatial projection of differing dominant-subordinate relationships. Mosaics made up of small fish had less direct access to, and less control of, substrate than those mosaics consisting of larger fish. If limiting resources are substrate associated, dominance rank will determine growth and survival.

Dominance was also a major factor in male reproductive success. Females consistently spawned with the most dominant courting male in laboratory populations. Hence, dominant males spawned earliest in the reproductive season, and thus, most frequently.

Gauthreaux (1978) has invoked dominance rank as an underlying regulatory factor in the population dynamics of a species through its effects on dispersal, differential habitat utilzation, the establishment and quality of an individual's territory, and reproductive success. Dominance has often been discussed within the context of social units, but not frequently when those units are territorial.

However, there has been an increasing appreciation of continua in behaviour, and the expression of dominance hierarchies and territories in the same social context is becoming more recognized (Greenberg 1947, Myrberg 1972).

Reproduction in *C. nicholsi* occurs for five months of the year. Therefore, it is a long-term factor in social organization and space use. Reproductive behaviour in this species is typical of gobiids (Breder and Rosen 1966). Gravid females enter the territory of a courting male, oviposit on the roof of the nest chamber, and return to their own territory. Males guard the eggs until they hatch. The larvae are planktonic.

The role of male dominance and spawning success, and the effect of reproduction on territory size of dominant males have already been discussed. Less is known about the reproductive and social roles of females and small males. Competition among females of *C. nicholsi* has not been documented, but as has been found in sticklebacks (Li and Owings 1978), it probably exists. Females of *C. nicholsi* can control the movements of smaller fish to some extent, through dominance effects. Therefore, females may interfere with smaller females' attempts to approach a large male to spawn. Females may also actively compete among themselves for territories located near those of large males. Direct access to spawning males would reduce the risk of predation while outside familiar territory. Thus, proximity to large males could be a major factor in female reproductive success.

Small males were never seen to court females. However, the testicular development of small males and their behaviour when near spawning pairs suggest that small males may employ sneaking as a means of achieving some reproductive success. If this is so, small males also benefit from defending a territory in close proximity to large males that frequently spawn and have high reproductive success. Thus, the defence of interstitial territories by fish adjacent to the territories of larger fish may not only provide refuge, but also enhance reproductive success.

Another aspect of reproduction and social organization in *C. nicholsi* is the occurrence of protogynous hermaphroditism. Females have the ability to change to functional males. The social conditions that typically favour sex change in other species appear to occur in *C. nicholsi*. Because females preferentially spawn with large males, large males have greater reproductive success than small males. This assumes that sneaking is not as productive as the conventional means of spawning, although the extent that small males contribute to the gene pool each reproductive season is unknown. Because large males are polygynous, large males probably have greater potential reproductive success than do large females. Accordingly, based on dominance effects, it is probable that among small fish, females have the greatest reproductive success.

The occurrence of sex change will have a profound effect on the social structure of this species. Instead of an equal sex ratio, two thirds of the population is female. Moreover, most small fish are female and most large fish are male. Hence, advantages of dominance, including access to space, are biased towards males. The sexual roles of fish are not fixed, because of the ability of females to change sex. For large males, an adjacent conspecific may be a highly desirable mate one year, and a reproductive competitor the next. Thus, social relationships among conspecifics based on dominance and sex are both subject to change.

Thresher (1977) has suggested that the variability of social organization among site-attached reef fishes may primarily reflect the effects of resource abundance and defensibility. In *C. nicholsi*, territories are multifunctional; they provide sites for reproduction, feeding and refuge. The universal defence of territory in a species which demonstrates uniparental behaviour and seasonal reproduction suggests that the primary defended resource is not a reproductive site. However, the occurrence of sex change in some females and the possibility of sneak spawning by small males makes it difficult to determine the importance of territories for reproduction to all adult males and females. Without adequate information on reproductive success among the fish within a given population, the relationship between reproduction and long-term territoriality cannot be assessed.

Fish obtained planktonic and benthic prey within their territories. The size of territories varied with fish size; and there was some indication that fish showing territorial overlap did not compete for the same food resource. But as no adequate measure was made of food abundance, its potential as a limited and defensible resource is unknown. Yet, apparently adequate feeding areas adjacent to occupied habitat were not occupied by *C. nicholsi*. Hence, feeding alone does not appear to be the major factor determining permanent territoriality in this species.

Cover, evidently important in both the field and laboratory situations, appeared to be the principal determinant in site selection. Territorial overlap rarely included areas containing cover. In laboratory populations, the location of structures offering cover governed site preference in the establishment of territories. In the field, areas without cover were unoccupied, but the introduction of cover to such areas led to rapid colonization by both small and large, adult *C. nicholsi*. Without the use of cover to avoid displacement by strong water action, for protection from predators, and for nocturnal refuge, survival appeared low.

C. nicholsi demonstrates permanent space defence by all members of the population, following settlement. The control of space appears to be behaviourally regulated by direct aggression and effects of dominance. The distribution of territories is dependent upon several factors, including fish size, dominance rank, and the time of year. This study shows that spatial and behavioural relationships among conspecifics are complex. It is these relationships, in combination with limitations of substrate-related resources, that control the social structure of this species.

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